Factors contributing to the spatial variation of stream communities in boreal and tropical regions

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ACADEMIC DISSERTATION
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Abstract

Freshwaters harbour disproportionally high biodiversity in relation to their area. Yet, they are among the most threatened ecosystems on Earth due to the increasing anthropogenic pressures. The ongoing climate change and Holocene extinctions give rise to an increasing need for conservation efforts in order to avoid future species losses. Successful conservation attempts require a comprehensive understanding how species and communities are distributed in space and time. There are notable gaps in the knowledge of diversity gradients of hyperdiverse microbes and invertebrates, and this knowledge gap is more pronounced in the tropics.

This thesis seeks to 1) investigate the effects of local environmental, catchment characteristics, spatial and climatic factors on stream communities across sites and catchments; 2) examine benthic diatom diversity patterns and the underlying factors within and among streams and stream orders; 3) examine the effect of environmental heterogeneity on benthic diatom beta diversity and; 4) compare the diversity patterns of stream diatoms and insects between boreal and tropical regions. To accomplish these aims, microbial and insect communities were collected from boreal and tropical regions and the underlying causes of community spatial variation were investigated using advanced statistical methods.

The thesis demonstrated that stream communities are driven by a range of factors acting on multiple spatial scales. Water chemistry, stream physical variables, biotic interactions, land use, spatial and climatic factors contributed to the variation in stream community composition and taxonomic richness. Diatom community composition exhibited significant within- and among-stream variation at intermediate spatial scales, which has relevance for biomonitoring using diatoms. Headwater streams exhibited higher beta diversity and harboured regionally unique diatom communities, which encourages the conservation of headwater streams. It was further demonstrated that environmental heterogeneity promotes diatom beta diversity, which emphasizes the role of habitat heterogeneity in sustaining diverse communities.

Somewhat surprisingly, diatom species richness was not higher in the tropics than in the boreal study region, and a notable number of diatom species were found from both regions. This implies that diatoms may not follow the traditional global latitudinal diversity gradient and further suggests that some diatom species exhibit global distributions. Insect genus richness was slightly higher in the tropics than in the boreal study region, whereas insect abundance was significantly higher in the boreal than the tropical region. The large within-region variation in insect genus richness and abundance may be more strongly driven by factors operating at regional scale than by the region itself, further suggesting that streams exhibit uniqueness and do not fit well into predefined categories based purely on latitude.

In summary, this thesis increases knowledge of the underlying variables affecting stream community variation. Further, biomonitoring and

conservational efforts may benefit from the identified factors contributing to regional stream diversity. Finally, this thesis increases knowledge and understanding of the similarities and differences of stream communities across regions.

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Going through the PhD-process has truly been the most educational and rewarding experience. Finishing a doctoral thesis can require blood, sweat, tears and stamina and, yet, all that will hardly lead into a desirable outcome without proper supervision. I was lucky enough to get first-class supervision and thus, first and foremost I express my deepest gratitude towards my supervisor Prof. Janne Soininen who has relentlessly guided me through this process. His scientific expertise and devotion to supervision has been outstanding by any standards. I could always trust his support and patience no matter how vague my questions and ideas were.

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In Helsinki, January 2nd 2018

Jenny Jyrkänkallio-Mikkola

Contents

List of original publications

This thesis is based on the following publications:

I **Jyrkänkallio-Mikkola J**., Heino, J., Soininen, J. (2016) Beta diversity of stream diatoms at two hierarchical spatial scales: implications for biomonitoring. *Freshwater Biology,* 61, 239–250.

II **Jyrkänkallio-Mikkola, J**., Meier, S., Heino, J., Laamanen, T., Pajunen, V., Tolonen, K. T., Tolkkinen, M., Soininen, J. (2017). Disentangling multi-scale environmental effects on stream microbial communities. *Journal of Biogeography*, 44, 1512–1523.

III **Jyrkänkallio-Mikkola, J**., Siljander, M., Heikinheimo, V., Pellikka, P., Soininen, J. Tropical stream diatom communities — the importance of headwater streams for regional diversity. Minor revision in *Ecological Indicators*.

IV Heino, J., **Jyrkänkallio-Mikkola, J**., Tolonen, K.T., Melo, A.S., Petsch, D.K., Bini, L.M., Saito, V.S., Soininen, J., Siqueira, T. Convergence and divergence of stream insect richness and abundance patterns between tropical and boreal regions. Manuscript.

Henceforth, the publications are referred to by their roman numerals.

Authors' contributions

	Paper I	Paper II	Paper III	Paper IV
Original idea	JH	JH, JS, JJ	JJ, JS	JH, JJ, JS, TS
Study design	JH	JJ, JH, JS	JJ	JH, JJ, TS
Field and laboratory work	JH, TK	JJ, VP, SM, KT, MT, TL	JJ	JJ, VP, SM, KT, MT, TS , DP
Data analysis	JJ	JJ, VP, TL	JJ, MS,VH	JH, KT, DP, VS
Writing the article	JJ, JH, JS	JJ, SM, JH, TL, VP, KT, JS	JJ, MS, VH, PP, JS	JH, JJ, DP, VS, KT, LB, AM, JS, TS
Overall responsibility	JJ	JJ	JJ	JH

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Abbreviations

AIC	Akaike's information criterion
ALS	Airborne laser scanning
BRT	Boosted regression trees
CAP	Canonical analysis of principal coordinates
CHM	Canopy height model
dbMEM	Distance-based Moran's eigenvector maps
db-RDA	Distance based redundancy analysis
DEM	Digital elevation model
GDD	Growing degree days
GSP	Growing season precipitation
ICP-OES	Inductively coupled plasma-optical emission spectrometry
LCBD	Local contribution to beta diversity
LM	Linear regression analysis
m a.s.l.	Meters above sea level
OTU	Operational taxonomic unit
PCNM	Principal coordinates of neighbour matrix analysis
PERMDISP	Tests of homogeneity of dispersion
RCC	River continuum concept
RDA	Redundancy analysis
TN	Total nitrogen
TP	Total phosphorus
VP	Variation partitioning
WAB	Water balance

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1 Introduction

The total number of species on Earth is predicted to be around 8.7 million excluding prokaryotes (Mora *et al*. 2011). Throughout Earth's history, extinctions have always been an integral element of evolution. However, the rapid growth of human population has resulted in an increase of extinction rates of 100 – 1000 times of that before the emergence of humans (Pimm *et al*. 1995). A recent study reported that the decline of sizes and ranges of natural populations is even more severe than previously thought (Ceballos *et al*. 2017). The extinction threat applies to a range of species, with both terrestrial and aquatic species being under threat. The ongoing climate change and Holocene extinction urge to put a great emphasis into conservation efforts in order to avoid future species loss, which requires a thorough understanding how species and communities are distributed on Earth in space and time.

1.1 Freshwaters and streams

Freshwaters cover only about 0.01% of the Earth's surface (Balian *et al*. 2008), yet these environments harbour disproportionally high species richness in relation to area, which is almost 6% of all the recognized species (Dudgeon *et al*. 2006). Until recently, there has been a notably stronger emphasis on studies focusing on terrestrial and marine diversity gradients compared to freshwaters (Boyero 2002). This knowledge gap is especially pronounced for invertebrates and microbes, and is even more emphasized in the tropics, which also ironically cradles most of the biodiversity on Earth (Dudgeon *et al*. 2006).

Freshwaters provide various goods and services to humans (Wilson and Carpenter 1999) and, due to the increasing demands and effects directed upon them, are among the most threatened ecosystems on the planet (IUCN 2009, Strayer and Dudgeon 2010). The current biodiversity losses and future extinction rates in freshwaters are higher than in terrestrial or marine ecosystems and more pronounced in tropical than in temperate regions (Wiens 2016). The greatest threats compromising freshwater biodiversity are overexploitation, water pollution and eutrophication, flow modification, habitat degradation and invasive species (Dudgeon *et al*. 2006). The restoration costs for freshwater ecosystems, such as streams, have been substantial (Palmer *et al*. 2005) and, thus, thorough knowledge of these ecosystems is of outmost importance. Conservation of freshwater biodiversity and ecosystems will be a great challenge under increasing human demands and activities (Vorosmarty *et al*. 2010, Wiens 2016).

Streams occur in a remarkable variety of forms, and differ substantially in terms of physical, chemical, riparian and catchment characteristics (Hynes 1970). The concept of stream order defines the fluvial hierarchic nature of the stream network in which the smallest perennial headwater streams are referred to as first order streams, and at the confluence of two first order streams they result in a second order stream and so forth (Fig. 1; (Strahler 1957, Allan and Castillo 2007)). Stream order correlates with many of the stream characteristics, such as catchment area, discharge volume and channel width (Allan and Castillo 2007), and anthropogenic stressors typically increase downstream (Lowe and Likens 2005). Stream order may also be a significant factor related with stream biotic communities (Finn *et al*. 2011).

1.2 Diversity patterns and components

Biodiversity shows globally strong geographical variation. The latitudinal diversity gradient

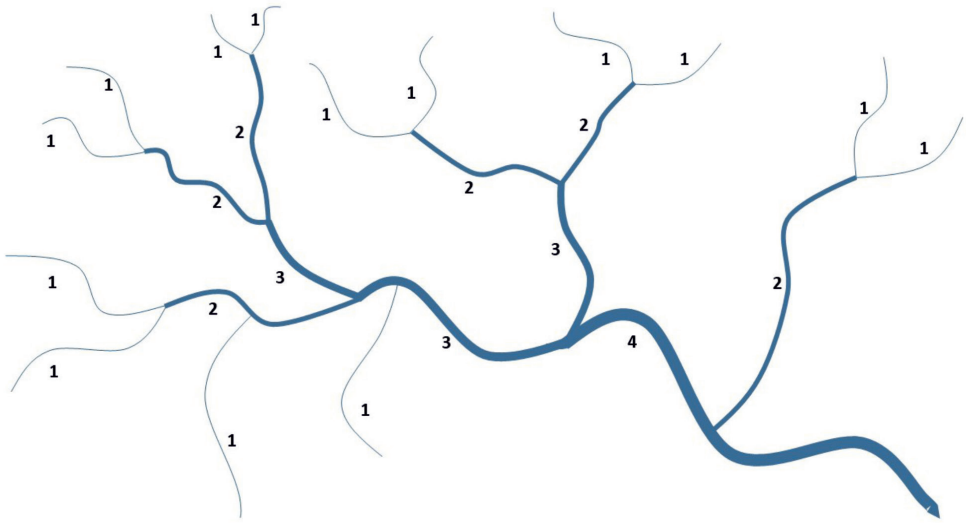


Figure 1. Schematic representation of the stream order concept after Strahler (1957)

suggests that more species are found closer to the equator than the poles (Rosenzweig 1995, Gaston 2000, Hillebrand 2004). This phenomenon is also evident in the fossil records, suggesting that the difference in the distributions of biodiversity has prevailed also through time (Buzas *et al*. 2002). A number of mechanisms have been put forward to cause this difference. These include models that lack any evolutionary or ecological explanations such as mid-domain model, which considers Earth to be geographically constrained for species ranges where the diversity peaks in the middle (equator), whereas the edges (poles) are more depauperate (Colwell and Lees 2000). Other models use latitude as a surrogate for many co-varying primary factors such as insolation, productivity, temperature and more, which also correlate and interact with one another (Hillebrand 2004). While latitudinal diversity gradients are comprehensively studied and well documented for several terrestrial macro-organisms (Hillebrand 2004), this phenomenon is still much debated for stream invertebrates (Stout and Vandermeer 1975, Flowers 1991, Jacobsen *et al*. 1997, Vinson and Hawkins 2003), as well as algae and micro-organisms in general (Hillebrand and Azovsky 2001, Fuhrman *et al*. 2008, Passy 2010, Salinas *et al*. 2015).

Biodiversity can be divided into three components. Alpha diversity measures local species richness, gamma diversity defines regional species richness and beta diversity measures between-site differences in species composition (Whittaker 1960). Beta diversity can be used to measure the community compositional variation in communities not only in space, but also in time (Soininen 2010). From all biodiversity components, beta diversity is the most useful measure to study the underlying processes that generate and maintain biodiversity (Legendre *et al*. 2005, Qiao *et al*. 2015, Socolar *et al*. 2016), yet it has received less attention at intermediate spatial scales (e.g. within and among streams in a catchment) or in the tropics (Brown 2014).

Alpha and gamma diversity are typically correlated in different taxa and continents (Caley and Schluter 1997), and great local species richness often reflects great regional richness (Hillebrand 2005, Boulton *et al*. 2008). However, different factors may contribute to regional and local rich-

ness. Areal extent, climate, productivity or history may contribute to regional richness (Willig *et al*. 2003, Mittelbach *et al*. 2007), whereas local richness might be more related to the differences of ecosystem physical and chemical characteristics (Vinson and Hawkins 2003, Heino 2011) and biotic interactions (Mod *et al*. 2016). For many understudied organisms, there is a limited amount of evidence whether the underlying factors contributing to regional and local species richness differ between biomes such as tropics and temperate or boreal regions.

1.3 Stream organisms

Like freshwaters in general, fluvial ecosystems also contribute to global biodiversity highly disproportionally in relation to their area (Allan and Flecker 1993, Vinson and Hawkins 1998, Vorosmarty *et al*. 2010). Whereas studies focusing on stream organisms are relatively numerous for boreal and temperate regions, only recently more emphasis have been placed on studying tropical stream macrobenthos (Heino *et al*. 2015b, Saito *et al*. 2015, Siqueira *et al*. 2015). Even less is known about tropical stream micro-organisms, but see Bellinger *et al*. (2006), Bere (2014), Bojorge-Garcia *et al*. (2014) and Mangadze *et al*. (2015). Hence, the focus of this thesis lies on these groups.

Benthic algae are primarily composed of diatoms (Bacillariophyceae) and green algae (Chlorophyceae), and to a smaller extent red algae (Rhodophyceae), chrysophytes (Chrysophyceae) and tribophytes (Tribophyceae) (Graham and Wilcox 2000). Typically benthic algae are also considered to include blue-green algae (Cyanobacteria). The association of benthic algae with auto-and heterotrophic bacteria and fungi that occur in the extracellular matrix on the submerged surfaces of rocks, sediment and vegetation, is referred to as biofilm (Allan and Castillo 2007). Cyanobacteria are significant photoautotrophs associated with the biofilm and may contribute notably to the primary production in aquatic environments (Havens 2008). Diatoms are widely used as bioindicators due to their sensitivity to physicochemical changes (Hill *et al*. 2000, Wang *et al*. 2005). Benthic algae are the most significant primary producers especially in small streams that receive sufficient amount of light (Minshall 1978) and in many medium–sized streams (Vannote *et al*. 1980). Biofilm is actively grazed by scraping macroinvertebrates, and the importance of this autochthonous source of nutrition to grazers may depend on the stream size and allochthonous inputs to the stream (Vannote *et al*. 1980) as well as biome (Davies *et al*. 2008). In addition to being an important source of food to higher trophic levels, stream microbial communities also drive nutrient cycling (Palmer *et al*. 2014) and stabilize sediment (Dodds and Biggs 2002), hence providing valuable ecosystem services. For example, bacteria, such as Actinomycetales, are important decomposers of plant matter in streams and hence, break down material into smaller compounds that can be further utilized by biota (Sinsabaugh and Linkins 1990).

Aquatic invertebrates are traditionally referred to as macroinvertebrates. The fluvial macroinvertebrate fauna includes metazoans larger than 0.5 mm and consists of many taxonomic groups, being mostly insects, but also incorporating crustaceans, molluscs, oligochaetes, planarians and leeches (Jacobsen *et al*. 2008). Most stream insects have amphibiotic life cycles, meaning that they spend their larval stage in water and the adult stage on land (Jacobsen *et al*. 2008). Stream insect communities are often dominated by five insect orders: mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), beetles (Coleoptera) and true flies (Diptera) (Vinson and Hawkins 1998, Lancaster and Downes 2013).

1.4 Variation in stream communities

The determinants of stream community variation can be divided into ultimate, intermediate, proximate and riffle scale factors (Fig. 2). These factors may affect stream communities via complex pathways (Pajunen *et al*. 2017), and the assembly mechanisms act at different spatial and temporal scales. Spatial scale has a substantial effect on the detection of ecological patterns and the underlying causal mechanisms (Levin 1992). Furthermore, the relationships between communities and controlling factors may be confounded by scale-dependent processes (Vinson and Hawkins 1998).

The key determinants may vary between stream organismal groups. For micro-organisms, their small sizes, short reproduction cycles and remarkable population densities enable effective passive dispersal (Finlay and Clarke 1999, Finlay 2002). Furthermore, local extinction threat is decreased by the capability of some microbial taxa to form dormant life stages (Green and Bohannan 2006). The apparent lack of dispersal barriers for micro-organisms led to a statement "everything is everywhere, but, the environment selects" by Baas Becking (1934), which assumes that microbial communities are shaped solely by local environmental factors and, consequently suggesting microbial cosmopolitanism. Indeed, there is a large amount of evidence of the importance of water chemistry variables, such as conductivity (Soininen *et al*. 2004, de Figueiredo *et al*. 2012), pH (Schauer *et al*. 2005, Kahlert and Gottschalk 2014) and nutrients (Dalu *et al*. 2017, Wang *et al*. 2017), for aquatic microbial communities. In addition to abiotic factors, biotic interactions such as competition, herbivory, parasitism, mutualism and commensalism may also be important determinants of stream microbial communities (Peterson *et al*. 1993, Burkholder 1996, McCormick 1996, Steinman 1996, Carr *et al*. 2005).

The pure environmental control on microbial communities is, however, challenged by the studies that found spatial (Cho and Tiedje 2000, Soininen *et al*. 2004, Martiny *et al*. 2006, Fuhrman *et al*. 2008) and historical (Vyverman *et al*. 2007) processes affecting microbial communities as well, which could imply that biogegraphic principles also apply to the microbial world. This contradiction may be caused by differences in the spatial extent of the studies (Verleyen *et al*. 2009, Van Horn *et al*. 2013, Heino *et al*. 2014, Maloufi *et al*. 2016). Indeed, a strong environmental control is often found from microbial studies conducted at small scales (Horner-Devine *et al*. 2004, Beisner *et al*. 2006, Martiny *et al*. 2006), whereas geographical and climatic factors are found to be important drivers of microbial communities on studies covering large geographical extent (Martiny *et al*. 2006, Verleyen *et al*. 2009, Heino *et al*. 2010). More uncertainty to this debate are added by the studies that found environmental variables to be the main controlling factors of microbial communities even at global scale (Van der Gucht *et al*. 2007, Soininen *et al*. 2016) and spatial processes to affect microbial community variation also at small spatial scales (< 60 m) (Meier and Soininen 2014). Community dissimilarity is expected to increase with increasing spatial distance as environmental differences typically grow with increasing geographical distance (Vetaas and Chaudhary 1998) and dispersal is weaker. Hence, spatial and environmental factors may jointly cause the variation in microbial communities (Heino *et al*. 2014, Soininen *et al*. 2016).

Stream insect communities are affected much by the same factors as stream micro-organisms at different spatial scales. Their community variation depends on local variables such as physi-

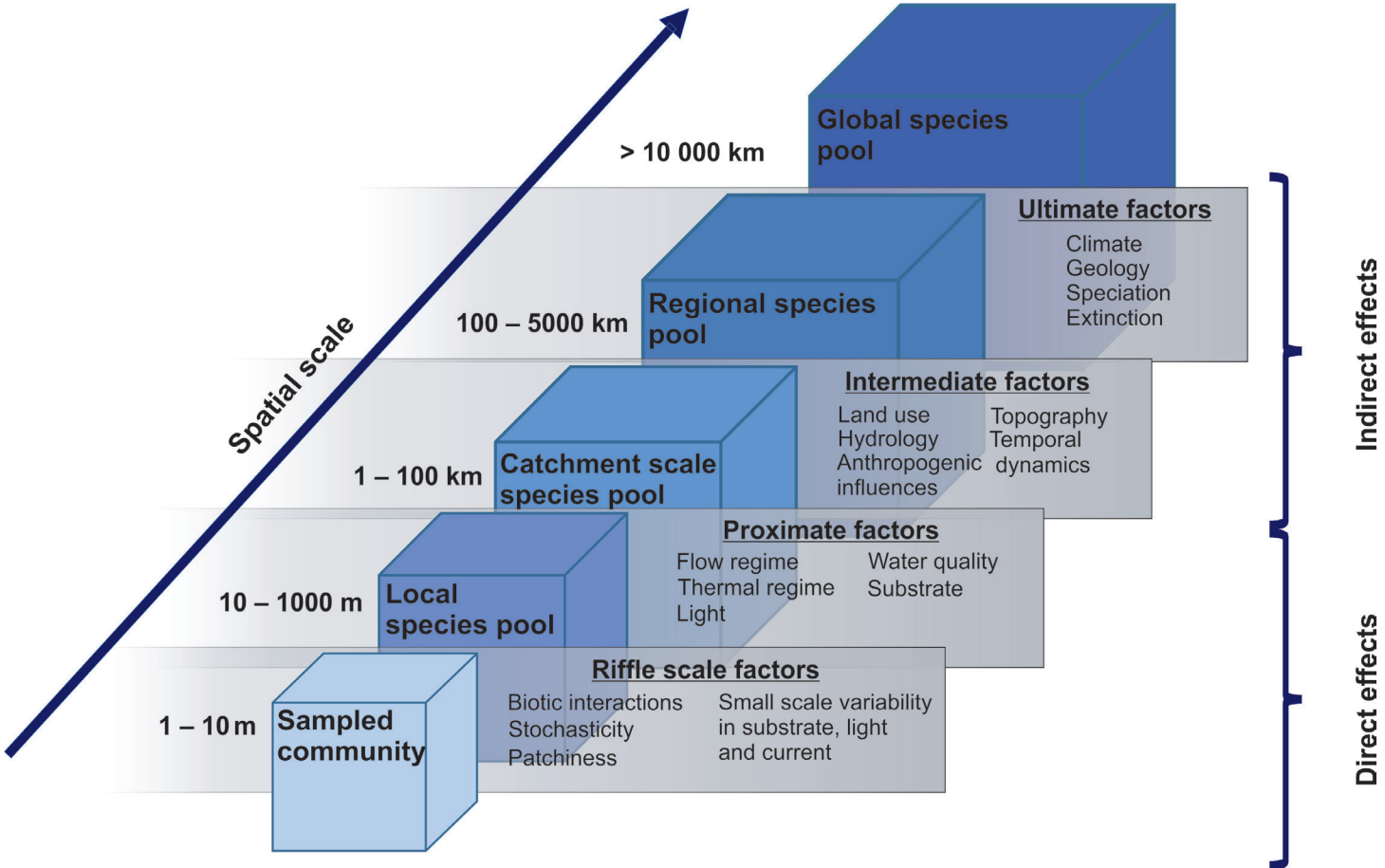


Figure 2. Schematic representation of the evolutionary and ecological factors underlying stream community assembly. Adapted and modified after Poff (1997), Stevenson (1997) and Gotzenberger et al. (2012).

cal variables of the stream, including substrate heterogeneity (Vinson and Hawkins 1998), habitat type (Scarsbrook and Townsend 1993), light (Hawkins *et al*. 1982), stream size (Minshall *et al*. 1985) and water chemistry (Jenkins *et al*. 1984, Smith *et al*. 1990). At a regional scale, factors such as biome (Donald and Anderson 1977), climate (Bhowmik and Schafer 2015), latitude (Stout and Vandermeer 1975) and continent (Lake *et al*. 1986) add variation to stream insect communities (Vinson and Hawkins 1998). Large–scale beta diversity of stream insect communities is likely to exceed that of microbial communities due to effects of geological history and dispersal ability on beta diversity (Astorga *et al*. 2012).

Stream biota may also be affected by environmental features acting at smaller scale. The River Continuum Concept (RCC) predicts species richness to peak in the middle section of the river network due to the more predictable thermal regime, whereas headwaters under the influence of larger variation in daily temperatures should be less diverse (Vannote *et al*. 1980). In addition to thermal regime, Stanford and Ward (1983) associated larger species richness in the mid-order streams to predictable discharge. Hence, these two predictions stem from the temporal variation in stream physical conditions (Vinson and Hawkins 1998). There is evidence for higher alpha diversity of mid-order streams (Sheldon 1988, Peres and Terborgh 1995), whereas patterns for beta diversity may be different, as headwater streams (orders 1 – 2) can harbour a large proportion of the biodiversity of the stream network (Meyer *et al*. 2007).

In general, environmental heterogeneity may be a significant driver for biodiversity (Stein *et al*. 2014) and also for fluvial ecosystems, which was proposed as early as the 1950s (Thienemann 1954). Environmental heterogeneity stems from the variation in physical and chemical environment, resources and biological interactions in space and time (Fig. 3; Palmer and Poff (1997), Seiferling *et al*. (2014)). In addition to spatial environmental heterogeneity, short- or long-term temporal heterogeneity (e.g. disturbance and stress) may also have profound effects on stream communities (Stevenson 1997). Biological patterns may stem from abiotic and biotic processes that act simultaneously (Palmer and Poff 1997), and the observed patterns and processes may be highly scale-dependent (Menge and Olson 1990, Levin 1992). Environmental heterogeneity has a notable importance in maintaining species richness (Beisel *et al*. 2000, Levin *et al*. 2001, Brown 2003, Davies *et al*. 2005), yet its effect on beta diversity is less clear (Heino *et al*. 2015c). As environmental homogenisation may lead to subsequent homogenisation in community composition (Stanford *et al*. 1996, Wyzga *et al*. 2011, Zeni and Casatti 2014), more emphasis should be placed in understanding its effects on beta diversity.

1.5 Thesis objectives

The main focus of this thesis was to study spatial variation of stream microbial and insect communities in boreal and tropical regions at different spatial scales and to unravel the underlying key factors behind the variation. Main objectives were:

- Q_1 Investigate the effects of local environmental, catchment characteristics, spatial and climatic factors on stream communities across sites and catchments (**I** – **IV**).
- Q_2 Examine benthic diatom diversity patterns and the underlying factors within and among streams and stream orders (**I**, **III**).

Q_3 Examine the effect of environmental heterogeneity on benthic diatom beta diversity (**I**, **III**).

Q_4 Compare the diversity patterns of stream diatoms and insects between boreal and tropical regions (**III**, **IV**).

Specific hypotheses are listed in table 1.

2 Material and methods

2.1 Study regions

The spatial scale of the study differed among the four papers ranging from intermediate scale (**I**) to comparisons between biomes (**III** and **IV**). Sampling area in paper **I** was located in north-eastern Finland in the Oulanka National Park (Fig. 1 in **I**) where 10 streams all draining into River Oulankajoki were sampled for benthic diatoms. The longest distance between the sampling sites was 18 km. Each stream included 10 sampled riffle sites, that is, there was a total of 100 sampling sites.

In paper **II**, the study area was notably larger covering approximately 500 km in north-south direction and 300 km in east-west direction stretching from Finland Proper to Northern Ostrobothnia (Fig. 4). Altogether 105 independent stream sites (i.e. one sampling site per stream) were collected for bacteria and diatoms (as well as stream insects to be studied in paper **IV**). There was notable variability in stream characteristics as shown in the surrounding photographs (Fig. 4).

Sampling area in paper **III** was located in Taita Hills in south-eastern Kenya (Fig. 5). Totally, 67 benthic diatom samples were collected using a sampling design that covered stream orders 1 – 5 so that several samples from the same connected river network were sampled. The largest distance between sampling sites was 63 km and the study sites covered an elevational gradient of 713 – 1929 m a.s.l. Streams varied in their characteristics as shown in the surrounding photographs (Fig. 5).

In paper **IV**, stream insects were collected from 100 independent streams from boreal and tropical biomes with strictly comparable sampling methods. Boreal study area was the same as used in paper **II**, but excluding five sites (coloured in red Fig. 4) in order to standardize the amount of total sample size on both biomes. Tropical study area was located in the state of São Paulo south-eastern Brazil and spanned 120 km in east-west direction and 70 km in north-south direction (Supporting information Fig. S1 in **IV**).

2.2 Field surveys

Fieldwork was carried out in September 2009 (**I**), in September 2014 (**II**) and January 2016 (**III**). For paper **IV** the boreal data set was collected in September 2014 and the tropical data between September and November in 2015. Sampling was done in autumn because macroinvertebrate sampling is advocated to be conducted in September – October in boreal and temperate regions due to the seasonal life cycles of many invertebrates (Wright 2000, Sporka *et al*. 2006). In temperate and boreal regions, macroinvertebrate abundance usually peaks in autumn and thus, it is the best time to collect samples especially if sampling is to be undertaken on only one occasion (Hill *et al*. 2016).

2.3 Biological sampling

Benthic diatom samples were collected using similar methods (**I** – **III**) by randomly choosing 10 cobble sized stones or bedrock and brushing the biofilm with a toothbrush using either a 3× 3 cm (**I**) or 5 × 5 cm (**II** and **III**) rubber tem-

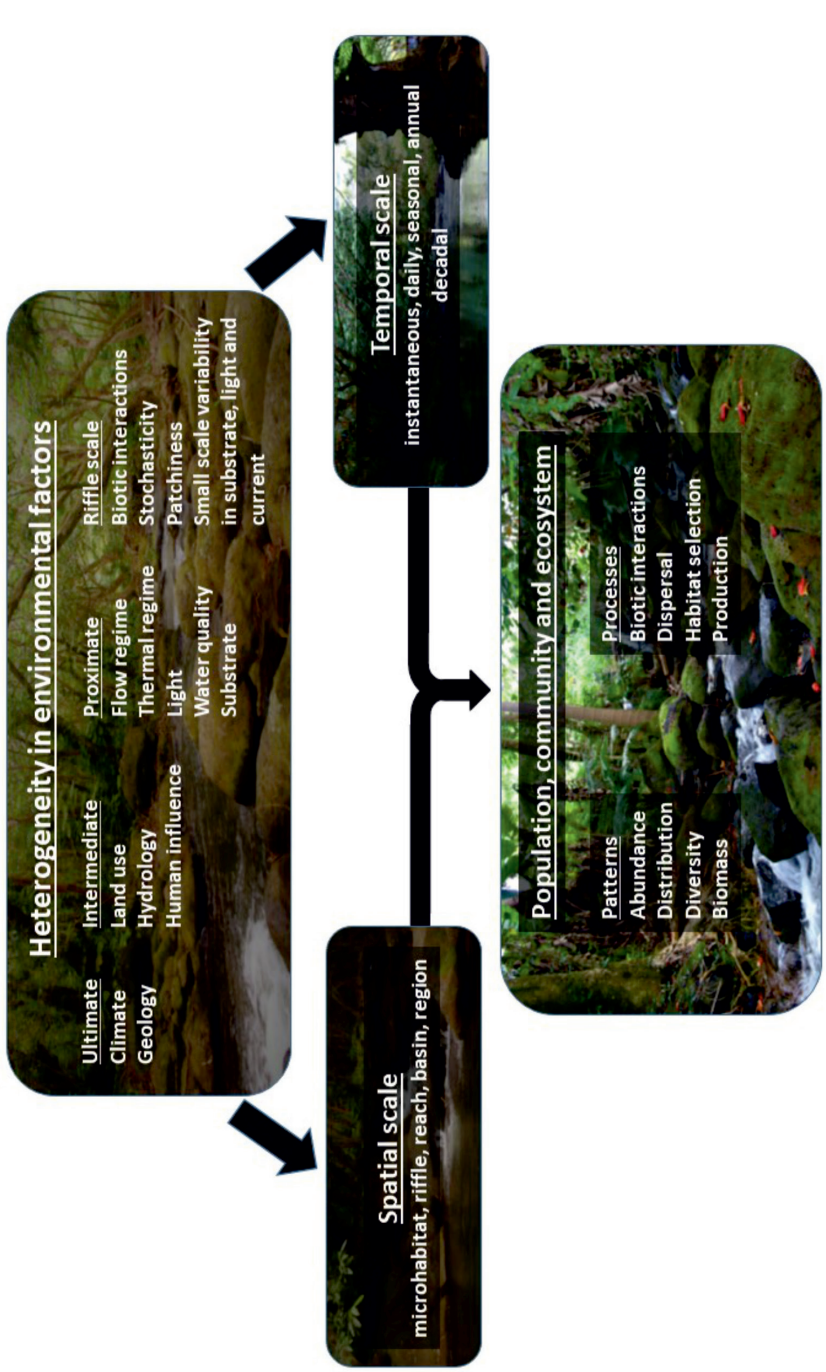


Figure 3. Conceptual representation of the influence of environmental heterogeneity on stream biota at different spatial and temporal scales. Adapted and modified after Palmer and Poff (1997).

Table 1. Hypotheses of the associations between the studied organisms and environmental or spatial factors. Not specified = the effect was studied but no specific hypothesis was set

Organism group	Diversity measure	Local environmental factors	Environmental heterogeneity	Land use	Spatial and climatic factors	Stream order	Biome
Bacteria	composition	Effective mostly at local scale, water chemistry in particular (de Figueredo et al. 2012, Schauer et al.2005, Wang et al. 2017). **II**	Not studied	Effective mostly at regional scale, agriculture in particular (Lear and Lewis 2009, Lear et al. 2013). **II**	Effective mostly at regional and continental scale (Cho & Tiedje 2000, Martiny et al. 2006, Fuhrman et al. 2008, Wang et al. 2012). **II**	Not studied	Not studied
	OTU richness	Not specified **II**	Not studied	Not specified **II**	Not specified **II**	Not studied	Not studied
Diatoms	composition	Effective mostly at local scale, water chemistry in particular (Soininen et al. 2004, Kahlert and Gottshalk 2014, Dalu et al. 2017). **I**, **II**, **III**	Not studied	Effective mostly at regional scale, agriculture in particular (Carpenter and Waite 2000, Bere and Tundisi 2011). **II, III**	Effective mostly at regional and continental scale (Soininen et al. 2004, Vyverman et al. 2007, Piano et al. 2017, Pajunen et al. 2016). **II, III**	Not studied	Not studied
	species richness	Conductivity and pH affect diatom species richness (Heino et al. 2010, Pither and Aarssen 2005). **II**, **III**	Not studied	Not specified **II**	Not studied	Larger streams harbour higher species richness than headwater streams (Meyer et al. 2007, Sherwood et al. 2000). **III**	Diatom species richness is higher in the tropics than in boreal region (Hillebrand 2004). **III**
	beta diversity	Not studied	Environmental heterogeneity promotes beta diversity (Astorga et al. 2014). **I**, **III**	Not studied	Not studied	Headwater streams show higher degree of beta diversity than larger streams (Finn et al. 2011). **III**	Not studied
Stream insects	genus richness	The same environmental variables are important for richness in boreal and tropical regions (Hynes, 1970; Allan & Castillo, 2007; Heino et al., 2003; Al-Shami et al., 2013. **IV**	Not studied	Not studied	Not specified **IV**	Not studied	Insect genus richness is higher in the tropics than in boreal region (Stout and Vandermeer 1975). **IV**
	abundance	The same environmental variables are important for abundance in boreal and tropical regions (Hynes, 1970; Allan and Castillo, 2007; Heino et al., 2003; Al-Shami et al., 2013). **IV**	Not studied	Not studied	Not specified **IV**	Not studied	More rare insect genera are found from the tropics (Leitão et al 2016). **IV**

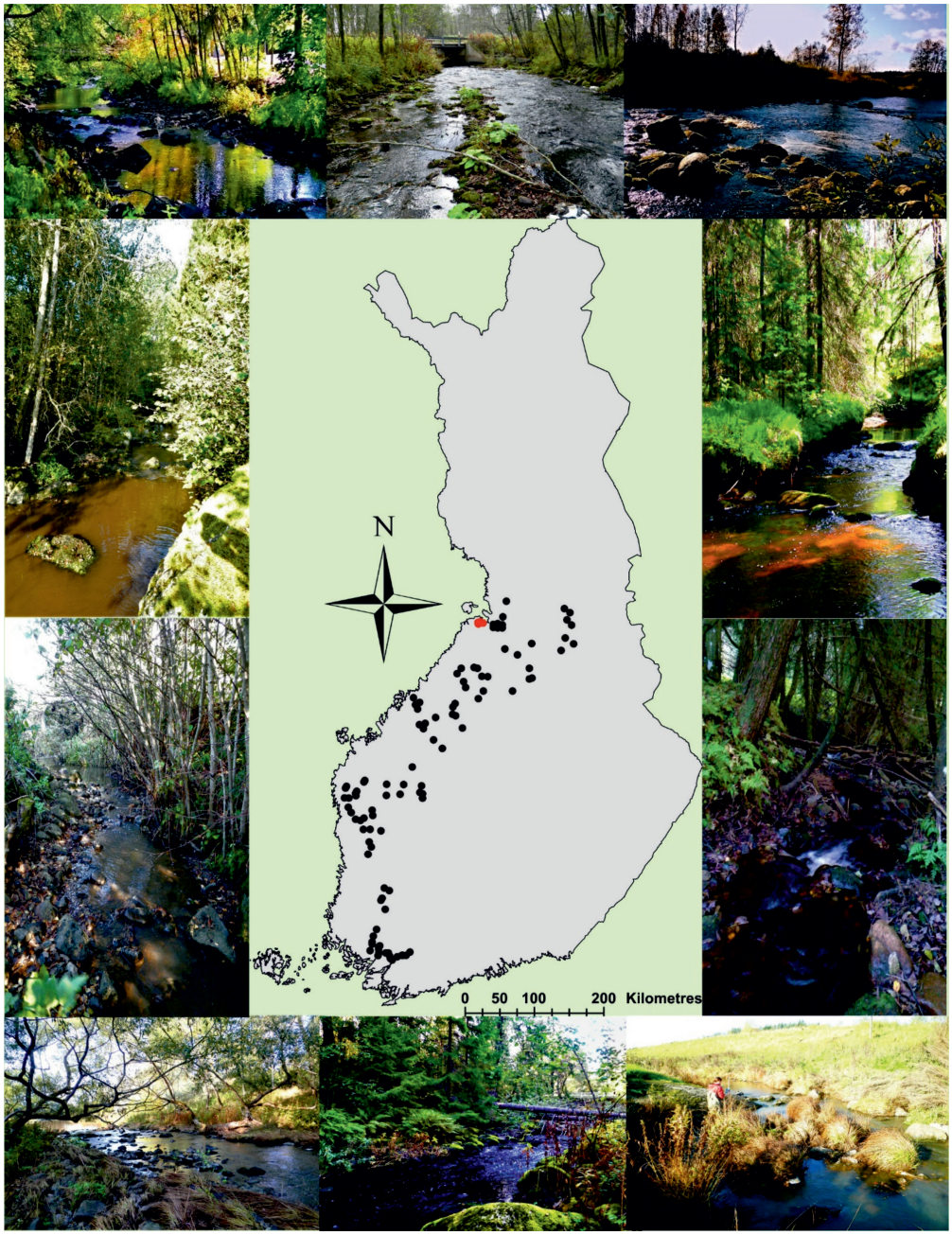


Figure 4. Map of the study area for stream microbes in paper **II**. Boreal insect data for paper **IV** were collected from the sampling locations excluding the sites marked with red colour.

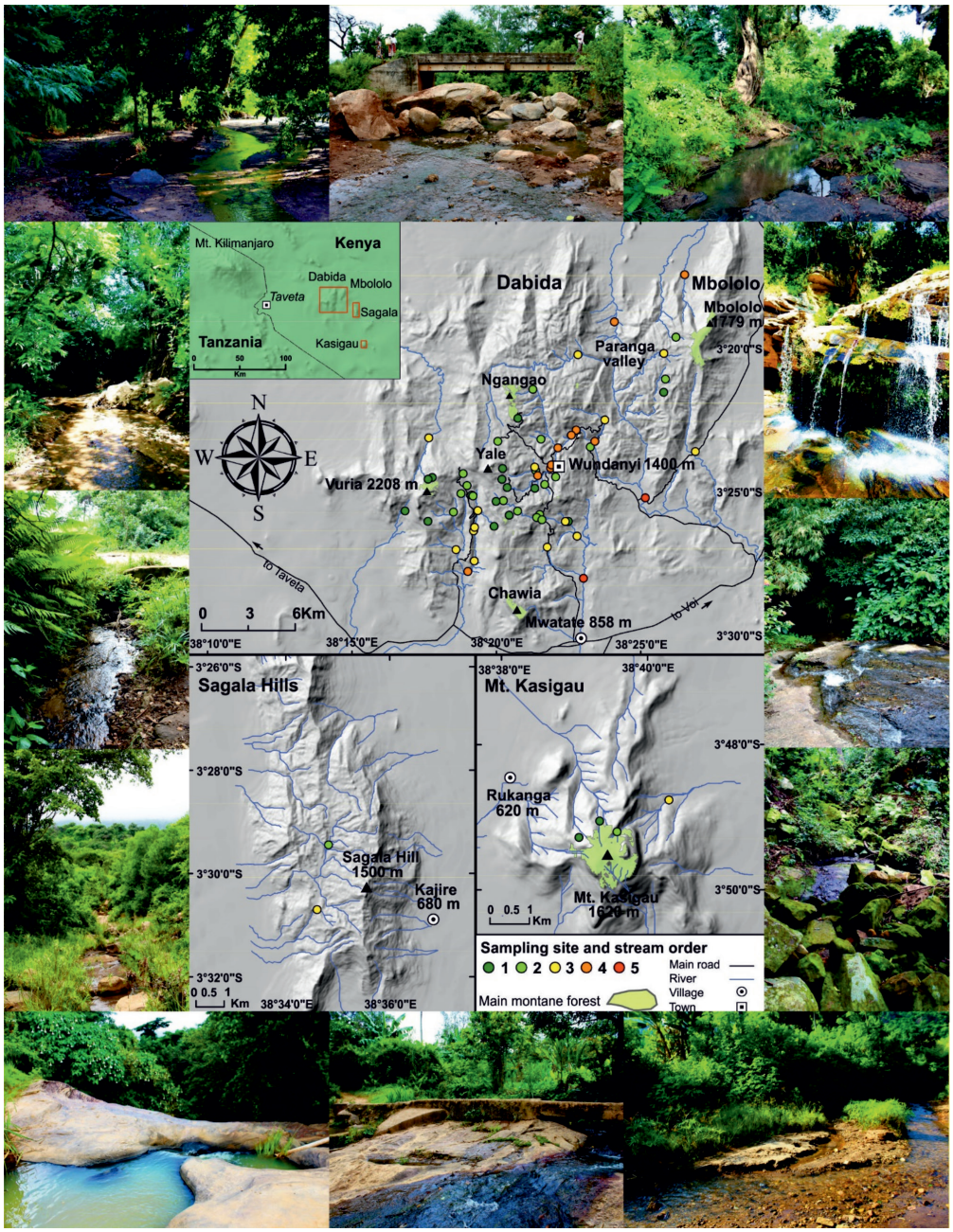


Figure 5. Map of the study area in Taita Hills, Kenya in paper **III**.

plate. Samples were preserved with ethanol the field and stored at +4°C. The organic material was removed from the diatom frustules by using wet combustion with acid (HNO_3: H_2SO_4; 2:1, (**I**)) or hydrogen peroxide (30%, H_2O_2, (**II**) and 20%, H_2O_2, (**III**)). Diatom frustules were mounted in Naphrax and at least 500 frustules were counted and identified based on Krammer and Lange-Bertalot (1986-1991), Lange-Bertalot and Metzeltin (1996) and Taylor *et al*. (2007) using 1000 × magnification in a phase contrast light microscope.

Bacterial samples (**II**) were rubbed from 10 different stones than the diatoms using sterile pieces of foam. Samples were frozen immediately until further analyses in the laboratory. PowerSoil DNA Isolation Kit (MoBio, Carlsbad, USA) was used to extract DNA from freeze-dried samples and bacterial 16S rDNA region was amplified with primers 519F 5′-CAGCMGCCGCGGTAATWC-3′ and 926trP1 5′-CCTCTCTATGGGCAGTCGGTGATC-CGT CAATTCCTTTRAGTTT-3′. Different unique a-primers for each sample were used. The PCR conditions used for amplification were as follows: Stage 1, performed once (Step 1, 98°C, 3:00 min). Stage 2, repeated 30 times (Step 1, 98°C, 0:10 min, Step 2, 64°C, 0:30 min, Step 3, 72°C, 0:20 min). Stage 3, performed once (Step 1, 72°C, 5:00 min, step 2, 4°C, ∞). Ion torrent semiconductor was used to sequence the samples and Quantitative Insights Into Microbial Ecology (QIIME) pipeline version 1.8.2 (Caporaso *et al*. 2010) was used to determine the operational taxonomic units (OTUs; 97% similarity)

Stream insects (**IV**) were collected in both regions with similar sampling methods using a 2-minute kick-net sample with 0.5 mm net mesh size as four 30-seconds subsamples covering the riffle site (Mykrä *et al*. 2006). The samples at each site were pooled together and preserved with ethanol immediately until further processing in the laboratory. Insects were identified to the genus-level due to the challenges in species-level identification in the tropics and, thus genus-level identification enabled comparisons between the two regions. In general, macroinvertebrates are very incompletely known in most tropical regions (Jacobsen *et al*. 2008). The genus-level approach was appropriate, as according to Hubbell (2001), the richness relationships from species to family level are conserved for the majority of organisms. Also, the main community patterns are typically preserved at the species, genus and family levels in stream macroinvertebrates (Heino 2008).

2.4 Water chemistry

In the field, conductivity and pH were measured using YSI-plus professional water quality meter (YSI Incorporated, Yellow Springs, USA) (**II**, **III** and **IV** (boreal data)). For the tropical sampling sites in paper **IV**, conductivity and pH were measured with Horiba device U-50 series. For total nitrogen (TN), total phosphorus (TP) and water colour, samples were taken a few meters upstream from the sampling site and further analyzed in the laboratory. For paper **II** and boreal samples in paper **IV** standardized methods (EN ISO11905-1 (1998) for TN and EN1189 (1996) for TP) were used. In paper **III**, TN was measured using alkaline persulfate digestion where alkaline oxidation is carried out in a thermo digester and the converted TN quantified colorimetrically, whereas TP was measured with inductively coupled plasma emission spectrometry (ICP-OES). In paper **IV**, TN and TP for tropical samples were measured using Brazilian national standards (Golterman *et al*. 1978, Mackereth *et al*. 1978). Water colour was measured using EN ISO7997 (**II** and **III**). In paper **I**, emphasis was placed on the physical variables' effect on the diatom communities. Water chemistry variables

were measured in every stream from the up-most and down-most riffle sites and therefore could not be used in subsequent multivariate analyses that used riffle sites as study units. Moreover, in the absence of point sources of nutrients and pollutants, water chemistry between these points did not vary notably (Heino *et al*. 2013).

2.5 Physical analyses

Current velocity was measured from 40 locations (**I**) and 30 locations (**II**, **III** and **IV** (boreal data)) using Schiltknecht MiniAir2 (Schiltknecht, Gossau Switzerland), whereas Flowatch flow meter (JDC Electronic SA, Yverdon Switzerland) was used for tropical insect data and current velocity measured from 9 locations (**IV**). Stream depth was measured with a yardstick from 40 locations (**I**), from 30 locations (**II**, **III** and **IV** boreal data set)) and from 9 locations for the tropical insect data (**IV**). Stream width was measured with a measuring tape from 5 locations (**I**), 10 locations (**II**, **III** and **IV** (boreal data set)) and from 3 locations to support tropical insect data (**IV**).

In every paper, the stream substratum particle size and moss cover were visually classified from 10 locations with 50 × 50 cm quadrant placed randomly in each riffle site using modified Wentworth scale: sand (diameter 0.25 mm – 2 mm), gravel (2 mm – 16 mm), pebble (16 mm – 64 mm), cobble (64 mm – 256 mm) and boulder (>256 mm) (Wentworth 1922). Percentage of shading provided by canopy cover was visually estimated based on the individual estimates of the field workers. This was done along 50 m stretch of the riparian zone on both banks (**I**), from 20 locations across the riffle site (**II**, **III** and **IV** (boreal data)) and from 3 locations to support tropical insect data (**IV**). In addition, the percentages of deciduous trees were visually estimated on both sides of the river banks (**I**, **II** and **IV** (boreal data set)).

2.6 Spatial, stream order and climatic data

The methods used for obtaining spatial and climate data are presented in the original papers in detail. To delineate catchment areas for sampling sites patterns of flow direction and accumulation were calculated using digital elevation models (DEM) (grid resolution 10 × 10 m, National Land Survey of Finland 2013, **II**). In paper **III**, DEM data was acquired with different methods for different parts of the study area. DEM for Taita Hills and Kasigau area was based on airborne laser scanning (ALS) data sets (resolution of 1 × 1 m), which were obtained in 2013 and 2014 (**III**). For Sagala sampling sites, DEM was based on scanned 1:50 000 scale topographic map, which was created by digitalizing the contour lines that were converted to 10 m resolution raster DEM. DEM was further used to calculate river network and stream ordering with Strahler method (Strahler 1957). The DEM layers were further resampled into 10 m pixel size to harmonize the elevation models after which stream ordering and networks were recalculated. ArcGIS hydrological modelling tools were used for watershed delineation and stream order determination.

Land cover and superficial soil cover classifications for the catchment areas (**II**) were acquired from CORINE Land Cover data (20 × 20 m, (Finnish Environment Institute 2013)) and Soil map 1:200 000 (20 × 20 m, (Geological Survey of Finland 2012)). Evenness of catchment characteristics was further calculated to indicate heterogeneity of land use in each catchment:

$$E = D/Dmax$$

where D is the Simpson's D for land use and soil classes, which are divided by the total number of classes.

In paper **III**, land cover for the three massifs was assessed separately. Land cover classification for Taita Hills sampling sites was based on a 20 × 20 m resolution SPOT 4 satellite image from 23 October 2011 (CNES 2013), which was further classified into 9 land cover classes (Heikinheimo 2015) using methodology from Clark and Pellikka (2009). For Sagala area, land cover for catchment areas was classified using Sentinel-2A MSI Level-1C satellite image from 8 October 2016, downloaded from the Sentinel's Scientific DataHub (ESA 2015) and RandomForest (Breiman 2001) classifier in R. Land cover was further classified into relevant classes of bush, fields, forest and impervious surfaces. Land cover for Kasigau catchment areas was obtained using the same Sentinel 2A satellite image as for Sagala area combined with canopy height model (CHM) and DEM from the ALS. Kasigau study area was further classified into highland and lowland zones based on the 1 m pixel size DEM to separate montane vegetation from lowland vegetation. ArcGIS Map Algebra tool was used to derive the land cover classes. Finally, land cover classes from the Kasigau and Sagala areas were harmonized to be comparable with the sampling sites from Taita Hills.

Climatic data for paper **II** was based on the averages of the years 1981 to 2010, and were acquired from the Finnish Meteorological Institute. The data was based on latitude, longitude and altitude of the sampling sites and calculated using multiple linear regression and downscaling climate data from a 10 × 10 km resolution grid to the study site (Finnish Meteorological Institute; (Venalainen and Heikinheimo 2002)). Growing degree days (GDD, defined as temperature >5˚C), growing season precipitation (GSP; sum from May to September) and water balance (WAB) were further used in following analysis due to their effects on stream diatom communities (Pajunen *et al*. 2016).

2.7 Statistical analyses

Advanced statistical methods were used to study the underlying causes of spatial variation in stream communities (Table 2). Multivariate analyses enabled simultaneous study of the linkages of highly complex community compositions and the underlying controlling factors. Taxon accumulation curves were used to study how well one riffle site represented total diatom species richness for the individual stream (**I**), whether more diatom species are found from tropical streams compared to boreal streams (**III**), and how the number of insect genera accumulated with increasing number of samples at regional scale (**IV**) (function specaccum in the R package 'vegan'; (Palmer 1990, Colwell and Coddington 1994)). Total species richness (gamma diversity) was extrapolated using first order Jackknife method (**I** and **III**; (Heltshe and Forrester 1983)) and using the method "exact" (**IV**; (Ugland *et al*. 2003)). Rank-abundance curves were used (**IV**) to study the most abundant insect genera separately in boreal and tropical regions (function rankabunplot in the R package 'BiodiversityR'; (Kindt 2016)).

The average differences in community and habitat structure between the streams were studied with canonical analysis of principal coordinates (**I**) (CAP; (Anderson and Robinson 2003, Anderson and Willis 2003)), which aims to find axes through multivariate cloud of points that are best at discriminating among a priori defined groups (Anderson *et al*. 2008). For biological data, Bray-Curtis (abundance) and Sørensen (presence-absence) coefficients were used, whereas for standardised habitat data Euclidean distance was applied. Null hypothesis was that there are no differences in group centroids between streams and was tested with permutation tests with 999 runs.

Spatial autocorrelations of environmental

variables as well as diatom and bacterial OTU richness were examined using Moran I correlogram using the R package 'pgirmess' (Giraudoux 2015) (**II** and **III**). Correlogram significance was tested at level $P \leq 0.05$ with applied Bonferroni correction (P/k, where k is the number of distance classes used). Spatial structures among sampling sites were analysed using principal coordinates of neighbour matrix analysis (PCNM; (Borcard and Legendre 2002, Borcard *et al*. 2004, Dray *et al*. 2006)) (**II** and **IV**) and distance-based Moran´s eigenvector maps (dbMEM; function dbmem in the R package 'adespatial'; (Dray *et al*. 2017)) (**III**). These methods create spatial eigenvectors derived from geographical coordinates, and eigenvectors showing positive spatial autocorrelation were used to model spatial effects in subsequent redundancy analyses (RDA; **II** and **III**) and in linear regression analysis (LM; **IV**).

Community-environment relationships were studied using distance based redundancy analysis (db-RDA; (Legendre and Anderson 1999)) (**I**) and RDA (**II** and **III**). Final models were chosen using forward selection of explanatory variables based on Akaike's information criterion (AIC; (Peres-Neto *et al*. 2006)) (**I**) and function ordiR2step with 200 permutations (**II** and **III**). LM was used to study the effects of chemical, physical and spatial variables on insect richness and abundance (**IV**). Variables for the final model were selected using forward selection procedure with two stopping rules (function forward.sel in the R package 'packfor' (Blanchet *et al*. 2008)).

Variation partitioning (VP; (Borcard *et al*. 1992, Liu 1997, Anderson and Gribble 1998); function varpart in the R package 'vegan' (Oksanen *et al*. 2015)) was used to study how much of diatom community variation could be explained by physical variables, stream identity and grazer abundance and their shared effects (**I**). VP was also used to examine the sole and joint effects of local, catchment level and spatial and climatic factors on diatom and bacterial communities (**II**). VP was further applied to study the pure and shared effects of chemical, physical and spatial factors on insect richness and abundance (**IV**), after which the significance of the pure fractions were tested using fraction tests (R package 'vegan'; (Oksanen *et al*. 2015)).

Tests of homogeneity of dispersion (PERMDISP; function betadisper in the R package 'vegan'; (Anderson 2006, Anderson *et al*. 2006)) was used to study beta diversity within streams (**I**) and within stream orders (**III**). In this analysis, ANOVA F-statistics is used to test among group differences from individual observation to their group centroid (Anderson *et al*. 2006). In paper **I**, both coefficients Bray-Curtis and Sørensen were used, whereas Sørensen was used in paper **III**. In both papers, Euclidean distances on standardised habitat variables were used. The null hypothesis of no difference in beta diversity between streams (**I**) and stream orders (**III**) was subsequently tested. PERMDISP was further used to relate beta diversity to environmental heterogeneity (**I** and **III**). LM was used to test null hypothesis of no relationship between the degree of beta diversity and habitat heterogeneity (Al-Shami *et al*. 2013, Heino *et al*. 2013). In all PERMDISP analyses, 999 permutations were used to test significant differences between groups.

The uniqueness of diatom communities was studied using local contribution to beta diversity (LCBD; function beta.div in the R package 'adespatial'; (Legendre and De Caceres 2013, Dray *et al*. 2017), **III**). Diatom abundance data were Hellinger-transformed (Legendre and Gallagher 2001) and the analysis was run with 999 permutations. Different components of beta diversity across stream orders were further tested with species turnover and nestedness (function beta.multi in the R package 'betapart' (Baselga *et al*. 2017)).

Boosted Regression Trees analysis (BRT;

Table 2. Summary of the studied organism groups, biomes, response and explanatory variables and methods used in papers **I** – **IV**. Abbreviations: n = number of sampling sites, CAP = Canonical analysis of principal coordinates, PERMDISP = Tests of homogeneity of dispersion, db-RDA = Distance based redundancy analysis, VP = Variation partitioning, LM = Linear regression analysis, OTU = Operational taxonomic unit, PCNM = Principal coordinates of neighbour matrix analysis, RDA = Redundancy analysis, BRT = Boosted regression trees, dbMEM = Distance based Moran´s eigenvector maps, LCBD = Local contribution to beta diversity

Paper	Organism group	Biome (n)	Response variables	Explanatory variables	Statistical analyses
I	benthic diatoms	boreal (98)	community composition, species richness, beta diversity, ecological guilds	stream identity, stream physical factors, grazer abundance, environmental heterogeneity	species accumulation curves, CAP, PERMDISP, db-RDA, VP, LM
II	benthic diatoms and bacteria	boreal (105)	community composition, species and OTU richness	local level: water chemistry and stream physical variables catchment level: land use characteristics and soil types spatial and climate level: climatic and spatial factors	Moran I, PCNM, RDA, VP, BRT, LM
III	benthic diatoms	tropical (67) boreal (67)	community composition, species richness, LCBD, beta diversity	water chemistry and stream physical variables, land use characteristics, spatial variables, stream order, environmental heterogeneity	species accumulation curves, dbMEM, RDA, LCBD, BRT, PERMDISP, LM
IV	stream insects	boreal (100) tropical (100)	local genus richness, local assemblage abundance	stream physical and chemical variables, spatial variables	genus accumulation curves, rank abundance curves, PCNM, LM, VP, BRT

(Elith *et al*. 2008)) was applied to study the effects of environmental variables measured from local, catchment and climate levels on diatom and bacterial OTU richness (**II**). BRT was further used to examine the effects of environmental variables on diatom species richness and LCBD-values (**III**), and applied to examine the insect richness-environment and insect abundance-environment relationships for both boreal and tropical regions separately (**IV**). BRT is a machine learning technique that can handle many types of data. The strengths of this method are that it automatically takes into account interactions between predictors, can handle non-linearity and has small prediction errors (Elith *et al*. 2008).

LM was used to study the effect of grazer abundance on diatom morphological groups (**I**). Linear and polynomial regressions were also used to study the relationships of the most significant variables affecting microbial species richness derived from BRT (**II** and **III**). LM was similarly used to relate the richness of the two microbial groups to evenness on land use classes and evenness of soil types (**II**) and to study the relationship between species richness and LCBD (**III**).

All statistical analyses were conducted in R, using base versions 2.15.3, 3.0.2 and 3.2.2 (R Development Core Team 2013) using packages ´adespatial' (Dray *et al*. 2017), ´betapart´ (Baselga *et al*. 2017), 'BiodiversityR' (Kindt 2016), 'dismo' (Hijmans *et al*. 2015), 'gbm' (Ridgeway 2013), 'packfor' (Blanchet *et al*. 2008), 'PCNM' (Legendre and Legendre 2012), 'pgirmess' (Giraudoux 2015) and 'vegan' (Oksanen *et al*. 2015).

3 Summary of the results of original publications

3.1 Paper I

The main focus in paper **I** was to study the variation in boreal benthic diatom communities within and across streams at intermediate spatial scale. First, how well one sampling site (riffle) represents the total diatom diversity of the stream was tested. Second, variation in diatom communities was studied at two hierarchical scales, within and among-streams. Third, the relationship between environmental heterogeneity and diatom beta diversity was studied. Finally, the key variables that cause variation in diatom communities were identified.

Results indicated that there was great variation in diatom community structure within streams. Species accumulation curves did not reach an asymptote and the estimated proportion of total species richness that 10 samples covered ranged between 73.4 and 81.9% (Fig. 2 in **I**), suggesting that one sample taken from one riffle site is insufficient to represent diatom diversity of an entire steam. In total, 260 diatom taxa were identified, and species richness varied from 17 to 59. *Achnanthidium minutissimum* and *Cocconeis placentula* were the two most abundant and common species in the samples. Both diatom communities and habitat conditions exhibited significant differences among the streams (Fig. 3a-c in **I**). However, the variation in diatom community structure across streams was greater than habitat heterogeneity across streams, i.e., the streams were more similar in terms of their environmental characteristics than their diatom communities. Within-stream beta diversity and environmental heterogeneity differed significantly among streams at the observed intermediate scale (Fig. 4 in **I**). However, environmental heterogeneity was not positively related to diatom beta diversity. Finally, significant relationships between diatom community and stream physical structure were observed, with moss cover, stream width and depth, cobbles, current velocity and shading being the most important variables (Fig. 5 in **I**). Furthermore, grazer abundance had a significant effect on diatom communities and, more precisely, a negative effect on the high-profile diatom taxa. All measured variables explained 26% of the community variation.

3.2 Paper II

Paper **II** addressed the environmental and spatial effects on boreal stream diatom and bacterial communities and species and OTU richness. This effect was studied on three levels: local environment including water chemistry and stream physical variables, catchment level encompassing land use and different soil types, and spatial and climatic level including spatial variables derived from PCNM and climatic variables GDD, GSP and WAB. Diatom species richness among sampling sites varied between 13 and 81 and, in total, 347 diatom taxa were identified. The number of bacterial OTUs among sampling sites ranged between 359 and 745, and total number of OTUs was 12308. Bacterial data encompassed 5282 singletons, whereas 91 diatom taxa were found from only one site. Variables from all three levels had significant effects on both microbial communities (Fig. 2 in **II**). RDA revealed that local level variables had significant effects on both microbial groups, highlighting the importance of water chemistry to these communities as pH, conductivity and TP were the most important local level factors for both microbial groups (Fig. 2a, e in **II**). However, physical factors were also significant for the communities, as percentage of cobbles and moss were important for both microbial groups. The most important

local level factors driving diatom and bacterial richness were pH and conductivity, respectively (Fig. 3a, d in **II**).

Catchment-level characteristics explained a slightly larger fraction of total variation in diatom communities (Fig. 2d in **II**), and from catchment variables, agriculture was the strongest determinant of variation in diatom community composition (Fig. 2b in **II**). According to BRT, agriculture was also the strongest determinant of richness of both microbial groups of catchment level variables (Fig. 3b, e in **II**). GDD and the first spatial variable derived from PCNM were the main determinants for diatom community composition (Fig. 2c in **II**). Of climatic variables, GDD was also the main determinant controlling diatom and bacterial richness (Fig. 3c, f in **II**). VP revealed that from all three levels spatial and climate level had the largest unique effect on both microbial communities (Fig. 2d, h in **II**). The measured variables explained 37.8% of the total variation in diatom community composition, whereas the explained variation was only 6.3% for bacterial community composition.

3.3 Paper III

In paper **III**, the focus was on tropical stream diatom diversity across different stream orders (1 – 5). First, the existence of latitudinal diversity gradient for benthic diatoms was tested with species accumulation curves and by using boreal data from paper **II** for comparison. Secondly, the effects of environmental, land use, and spatial factors on benthic diatom communities were tested. Thirdly, the beta diversity components of nestedness and turnover as well as factors contributing to species richness and uniqueness of the communities were examined. Finally, the relationship between environmental heterogeneity and diatom beta diversity was studied.

Altogether 297 diatom taxa were identified and the species richness between the sampling sites varied from 15 to 71. According to the results, species richness was not higher in tropical streams than in boreal ones (Appendix B in **III**). RDA revealed that local environmental and spatial factors jointly controlled tropical stream diatom communities (Fig. 2a in **III**). Water chemistry played a significant role in controlling diatom communities, but physical variables such as shading and stream substrate were important as well. Land use was also significantly related to diatom communities, as broad-leaved forests harboured different diatom communities than those with high conductivity (Fig. 2b in **III**). Depending on the model, the measured variables explained 14.4 to 15.9% of the total community variation. In headwater streams, species turnover was highest, whereas nestedness peaked in larger streams. Larger streams encompassed higher diatom species richness than headwater streams, whereas the uniqueness of diatom communities was significantly higher at headwater sites than in large streams (Fig. 3a, b in **III**). According to the BRT, the most important variables controlling diatom species richness were pH, temperature and conductivity (Fig. 4a in **III**). These variables were all positively correlated with diatom species richness. The most important factors contributing to LCBD were conductivity, temperature and water colour, of which the former two showed negative and the latter positive correlation with LCBD (Fig. 4b in **III**). Environmental heterogeneity peaked in higher-order streams (Fig. 5a, b in **III**) and was related to high diatom beta diversity.

3.4 Paper IV

The aim of paper **IV** was to study the degree of similarity in stream insect regional and local genus richness and abundance patterns between boreal (Finland) and tropical (Brazil) streams.

Firstly, it was examined whether there are differences between genus accumulation curves and rank-abundance distributions between boreal and tropical biomes. Secondly, the effects of physical, chemical and spatial variables on local insect genus richness and abundance were tested. A further aim was to study the differences and similarities in factors controlling variation in insect richness between the regions.

Only four genera were shared between the two regions: the mayfly genus Caenis, and the caddisfly genera Hydroptila, Oecetis and Oxyethira. The results revealed that regional stream insect genus richness was somewhat higher in Brazil (83) than in Finland (77) (Fig. 1a in **IV**). However, the regional abundance was much higher in the latter region (Fig. 1b in **IV**). Similarly, local genus richness was slightly higher in Brazil than in Finland (Fig. 4a in **IV**), and local assemblage abundance was much higher in Finland than in Brazil (Fig. 4b in **IV**). The two regions differed notably in terms of the contributions of different insect orders to regional genus richness and total abundance (Fig. 1 in **IV**).

According to the variation partitioning the factors contributing to genus richness and assemblage abundance differed between the regions, as physical and chemical factors explained more of the variation in Finland, whereas spatial variables were more important in Brazil. BRT revealed that the variation in local genus richness was partly driven by the same variables in both biomes, most significantly by stream width and depth. Variation in local assemblage abundance was, however, driven by different variables in each region. In Finland, assemblage abundance was controlled by current velocity, total nitrogen and shading, whereas in Brazil the most important factors were pH and stream width.

4 Discussion

4.1.1 The relationships between the results and original hypotheses

The results of the thesis showed that a wide range of factors affect stream communities, diversity and richness on multiple spatial scales. A general summary of how the results of the thesis reflected the original hypotheses is shown in Tables 3A and 3B. Most results supported the hypotheses, whereas some results showed opposite or unexpected patterns.

4.2 The effects of local environmental, catchment characteristics, spatial and climatic factors on stream communities (I – IV)

4.2.1. Water chemistry

Multiple factors affect stream microbial community composition and species richness. The summary of the different factors contributing to diatom diversity found in this thesis are shown in Fig. 6. Stream microbial communities are shown to be strongly controlled by water chemistry (Carpenter and Waite 2000, Telford *et al*. 2006, Soininen 2007, Bere and Tundisi 2011) and our results generally supported their important role (**II** and **III**). Water pH and conductivity had significant influence on diatom (**II** and **III**) and on bacterial communities (**II**). These two variables were also important for species richness for both microbial groups and for diatoms in boreal and tropical regions, which emphasises their global importance for stream micro-organisms. Total phosphorus was important in determining diatom and bacterial communities and water colour was a strong determinant for diatom communities in boreal streams (**II**), where humic content can be relatively high. In tropical streams, phosphorus

Table 3A. Summary showing how diatoms and bacteria were affected by different factors and how the results reflected the original hypotheses. The matches between the hypotheses and the empirical data are marked with following colours: green = concordance with the hypothesis, orange = disagreement with the hypothesis, blue = divergent or unexpected result. Abbreviations: GDD (growing degree days), GSP (growing season precipitation), WAB (water balance)

Organism group	Measure of diversity	Local environmental factors	Environmental heterogeneity	Land use	Spatial and climatic factors	Stream order	Biome
Bacteria	composition	Water chemistry and physical variables were significant drivers of bacterial community variation. At regional scale (>500km) local environmental factors were less important than spatial factors. **II**	Not studied	Land use explained slightly less of community variation than local level variables and agriculture did not have a significant effect on bacterial community variation. **II**	Bacterial communities were spatially structured at regional spatial extent. WAB and GSP were significantly related with bacterial community variation. Spatial and climatic factors explained the largest amount of community variation at regional (>500km) scale. **II**	Not studied	Not studied
	OTU richness	Water chemistry and physical variables affected OTU richness. Conductivity was significantly and positively related with OTU richness. **II**	Not studied	Agriculture was significantly and positively related with OTU richness. **II**	GDD was significantly and positively related with OTU richness. **II**	Not studied	Not studied
Benthic diatoms	composition	Water chemistry, physical variables and biotic interactions were significant drivers of diatom community variation. At regional scale (>500km) local factors were less important than catchment and spatial factors. **I, II, III**	Not studied	Catchment characteristics, especially agriculture and broad leaved forest, were significant drivers of diatom communities. At regional scale (>500km), land use explained a larger amount of community variation than local level factors. **II, III**	Diatom communities were spatially structured at regional scale. GDD, GSP and WAB were all significantly related to diatom community variation. Spatial and climatic factors explained the largest amount of community variation at regional (>500km) scale. **II, III**	Not studied	Not studied
	species richness	Water chemistry (especially conductivity and pH) and physical variables were important drivers of diatom species richness. **II, III**	Not studied	Agriculture was significantly related with diatom species richness as richness was highest at moderate agricultural influence. **II**	GDD was significantly and positively related to diatom species richness. **II**	Diatom species richness was significantly higher in large mid-order streams than in headwater streams. **III**	Diatom species richness was not notably higher in the tropics. **III**
	beta diversity	Not studied	Divergent effect based on the spatial extent of the study and inclusion of water chemistry into the explaining factors. **I, III**	Not studied	Not studied	The degree of beta diversity was higher in headwater streams than in larger streams. **III**	Not studied

Table 3B. Summary showing how stream insects were affected by different factors and how the results reflected the original hypotheses. The matches between the hypotheses and the empirical data are marked with following colours: green = concordance with the hypothesis, orange = disagreement with the hypothesis, blue = divergent or unexpected result. Abbreviations: TN = total nitrogen

Organism group	Measure of diversity	Local environmental factors	Environmental heterogeneity	Land use	Spatial and climatic factors	Stream order	Biome
Stream insects	genus richness	Stream width and depth were the most important local environmental determinants in both regions. In Finland physical and chemical variables were much more important than in Brazil. **IV**	Not studied	Not studied	Spatial variables were much more important in Brazil than in Finland. **IV**	Not studied	Local and regional genus richness was somewhat higher in Brazil than in Finland.**IV**
	abundance	Current velocity and TN were the most important local environmental variables in Finland, whereas pH and stream width had the biggest influence in Brazil. In Finland physical and chemical variables were much more important than in Brazil. **IV**	Not studied	Not studied	Spatial variables were much more important in Brazil than in Finland. **IV**	Not studied	Both regions had several uncommon genera. Local abundance was notably higher in Finland than in Brazil. **IV**

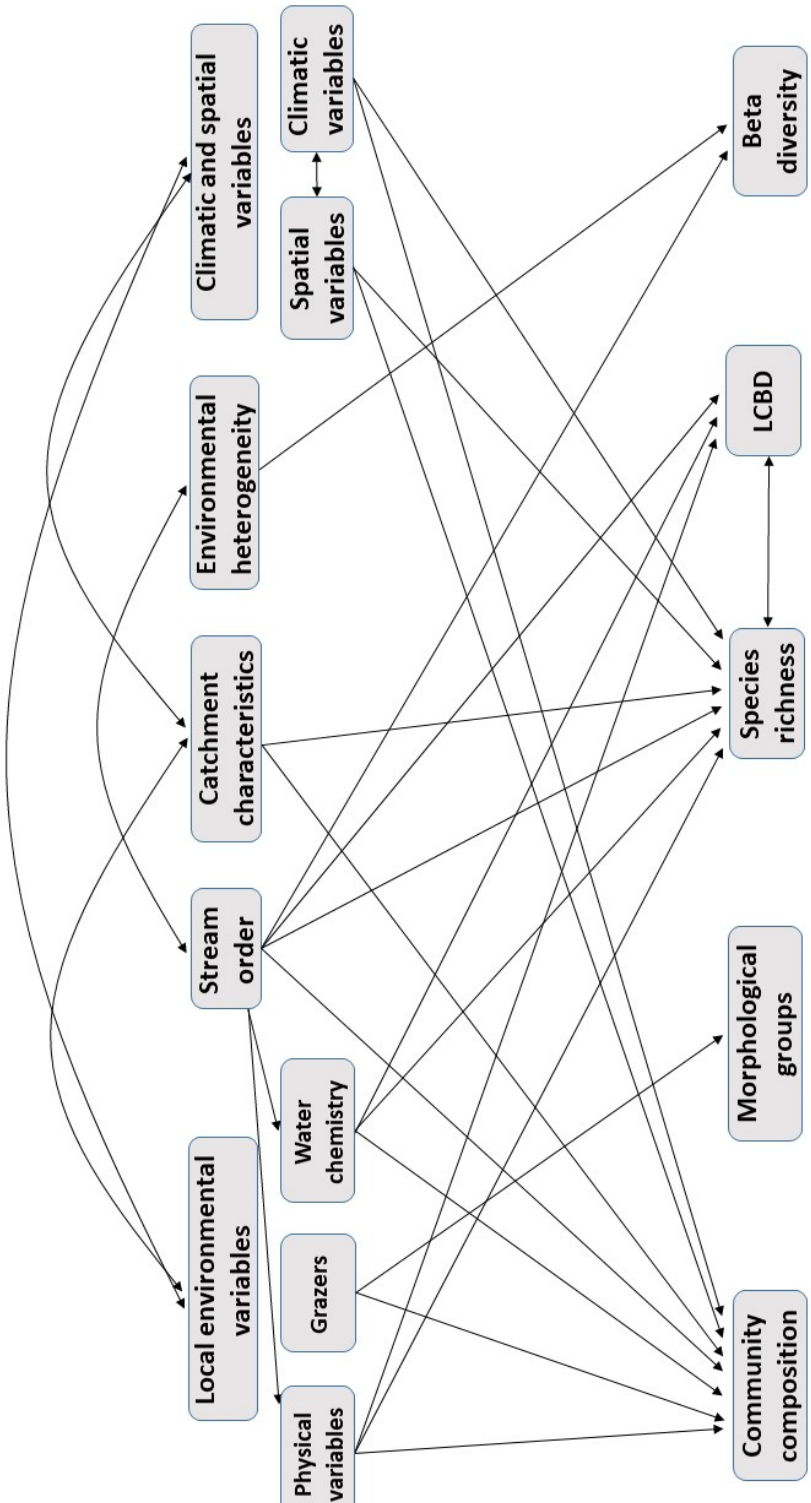


Figure 6. Summary of the factors contributing to benthic diatom diversity metrics examined in the thesis. One-sided arrows represent the most important effects and two-sided arrows correlations between the factors. Abbreviations: LCBD = local contribution to beta diversity

and water colour did not have a significant influence on diatom communities (**III**), which is most likely related to the low measured values of these variables (water colour: 0 – 50 Pt mgl^{-1}, TP: <10 – 69 μgl^{-1}). Typically, phosphorus and water colour affect diatom communities in different types of stream ecosystems (Raschke 1993, Fallu *et al*. 2002, Berthon *et al*. 2014).

Water chemistry variables had significant effects on local insect abundances, but their influence varied between Finland and Brazil, TN being important for insect abundance in Finland and pH in Brazil (**IV**). Overall, the insect abundances in these regions were controlled by different factors, which could be related to the lengths of environmental gradient within each region. As the pH range was similar in both regions, it may be possible that biological responses of stream insects to acidity may differ between tropical and temperate regions. Water chemistry may fluctuate rapidly in streams (Volkmar *et al*. 2011), and the fact that snapshot measurements cannot take this variability into account may decrease the explanatory power of these variables on the communities. Furthermore, the responses to water chemistry variables are likely to differ between specialist and generalist species, which is especially true for indicator species, as typically indicator species are also specialists. The measured range of an environmental variable has a notable influence on the importance of the variable on communities under study (Telford *et al*. 2006). This fact is important to be considered when the results are interpreted.

4.2.2. Physical variables

Water chemistry variables are not the only determinants of stream microbial communities, as stream physical variables such as moss cover, width, depth, current velocity, shading and substratum were also important drivers (**I** – **III**). Moss cover and varying substrate may add to the habitat complexity and stability of the stream bed. Boulders were among the most significant variables controlling diatom species richness (**II**) and, as greater number of boulders are typically found in larger streams, greater diatom species richness may be related to higher stream order (**III**) and is discussed further below. Shading and depth are correlates of the amount of light reaching to the bottom and, consequently, important to autotrophic organisms. Canopy cover as a correlate of shading was found to impact diatom communities in previous studies (Carpenter and Waite 2000, Bere and Tundisi 2011). Hydromorphological factors may play an important role in controlling stream diatom composition (Bere *et al*. 2016). Current velocity may act as a surrogate of disturbance regime and has been demonstrated to affect diatom community composition (Passy 2001, Schneck *et al*. 2017). This, however, may not be true for species richness and flood disturbance may further reduce the numbers of high-profile taxa more than other morphological groups (Schneck *et al*. 2017). High flow can also be linked to high turbidity, which reduces light availability for primary producers (Lewis *et al*. 1995). High flow disturbances also have profound effects on periphyton communities through scouring and resetting communities into early successional stage (Smucker and Vis 2013). Therefore datasets consisting of communities at different successional stages are likely to add uncertainty into the analyses.

Physical variables were more important in determining insect richness than water chemistry (**IV**). Stream size seemed to be the most important factor controlling insect genus richness, as it was positively related with stream width and depth in both regions and further supports RCC predictions (Vannote *et al*. 1980). Physical variables contributing to insect genus abundance varied between the regions as current velocity and shading were important in Finland, where-

as stream width was influential in Brazil (**IV**). The varying importance of shading may be more strongly related to the degree of human impact than study region, as it is an important factor for macroinvertebrate communities especially in pristine streams (Tonkin 2014).

Temporal fluctuations in stream physical variables can have a profound effect on community composition. For example, flow intermittency increases environmental heterogeneity and, as some species may be highly adapted to hydrologic stress (Stanish *et al*. 2012). Hence, flow intermittency can facilitate the persistence of endemic species. Short term variation in flow regime may be more pronounced in the tropics due to changes in atmospheric moisture (Lewis *et al*. 1995). Furthermore, the contrast between wet and dry seasons can have a great influence on stream communities in tropical systems (Douglas *et al*. 2005) even if winter is lacking from the tropics. As noted above, snapshot sampling cannot take into account temporal variations of physical and chemical factors, which is an unfortunate disadvantage. However, to cover statistically adequate amounts of samples and collect them frequently is costly, which usually hinders such efforts. There is thus always a tradeoff between spatially and temporally extensive sampling.

4.2.3 Biotic interactions

The results supported the view that biotic interactions can affect periphytic communities within a stream, as the amount of grazing invertebrates was the most significant variable structuring diatom communities (**I**). The number of grazers had different effects on diatom morphological groups, as high-profile taxa were negatively associated with the number of grazing invertebrates and thus, possibly more affected by grazing, whereas low-profile taxa showed positive correlation and motile non-significant relationship with grazers. Such selectivity by grazers towards certain algal species and growth forms was reported by Steinman (1996) and Rosemond *et al*. (2000). Rather than being actively selected, it is more likely that the negative effect of grazers on the high-profile taxa was more related to high-profile taxa being more subjected to grazing than attached low-profile taxa. However, the observed effect may not prevail throughout the year, as considerable seasonality as well as inter annual variation in the distribution and abundance of various invertebrate taxa is reported (Brooks 2000, Sporka *et al*. 2006, Leung *et al*. 2012). Thus, temporal variability in biotic interactions needs to be considered. Poff and Nelson-Baker (1997) found that snail grazing led to algal patchiness, but its effect was related to the spatial heterogeneity of the stream flow. Furthermore, grazing can act in concert with light, pH and nutrients (Rosemond *et al*. 1993, Lange *et al*. 2011, Gothe *et al*. 2013), which emphasises the complex nature of biotic interactions and how they are connected with the abiotic environmen

4.2.4 Land use

Catchment characteristics affect stream microbial communities at a larger spatial scale than local scale variables and can influence fluvial communities indirectly via water chemistry (Maloney and Weller 2011, Riseng *et al*. 2011). Catchment characteristics may reflect water chemistry at longer time scales and thus may be more robust determinants of biotic communities. In addition, they can also reflect some unmeasured variables. Diatom communities were affected by land use variables and most profoundly by agriculture (**II**) and broad-leaved forests (**III**), which indicates that diatom communities under anthropogenic influence differ from those in more pristine conditions, which is supported by previous studies (Carpenter and Waite 2000, Bere and Tundisi 2011). Bacterial communities

were affected by catchment characteristics (**II**), which is supported by (Lear and Lewis 2009) who found that stream bacterial communities differed significantly along land use gradient. In this thesis, bacterial communities were not related to the amount of agriculture, which is in contrast with results reported by (Lear *et al*. 2013).

Agriculture was the main factor controlling diatom and bacterial OTU richness at catchment level (**II**). Diatom species richness peaked under moderate agricultural influence, which suggests that intermediate perturbation by landscape alteration could promote species richness and furthermore gives support to the Intermediate Disturbance Hypothesis (Connell 1978). In addition, this result may reflect productivity-diversity hypothesis (Whittaker and Niering 1975, Tilman 1982) via nutrient increase. The positive relationship between bacterial OTU richness and the amount of agriculture may be related to the increase of anthropogenic stressors such as conductivity (Pajunen *et al*. 2017). In addition, deforestation and agriculture at the catchment area may change community composition, decrease diversity and eliminate sensitive taxa of stream communities at all trophic levels (Noel *et al*. 1986, Bojsen and Barriga 2002, Bojsen and Jacobsen 2003, Lorion and Kennedy 2009, Yu and Lin 2009, Siqueira *et al*. 2015). Harding *et al*. (1998) found that historic land use can have a profound effect on macroinvertebrate species richness. They further concluded that the recovery of stream diversity may be hindered for as long as decades by large-scale sustained agricultural activities in the catchment, which emphasizes the need to protect riparian networks from the detrimental activities of human induced changes in land use.

4.2.5 Spatial processes

Stream microbial communities were also spatially structured at spatial extents smaller than continental or global (**II** and **III**; (Martiny *et al*. 2006)). This finding may suggest that microbes exhibited dispersal limitation, which is likely to increase with increasing geographic distance, whereas environmental control should be stronger at smaller spatial scales (Martiny *et al*. 2006, Ng *et al*. 2009, Heino 2011). However, it is possible that mass effects (i.e. species are present also at unfavorable sites due to high dispersal rates (Shmida and Wilson 1985) rather than dispersal limitation contributed to the spatial component. This is expected at relatively small spatial extents (i.e. < 100 km), where sites are highly connected (Astorga *et al*. 2012), and mass effects can be caused by downstream drift of cells (Gothe *et al*. 2013). The spatial component may, indeed, be related to connectivity among sites and flow directionality (Liu *et al*. 2013, Zorzal-Almeida *et al*. 2017), as dissimilarities are likely to increase between communities inhabiting stream sections disconnected from one another (Piano *et al*. 2017). Whereas the mass effects may have caused the spatial patterns observed in paper **III**, this explanation seems unlikely for the spatial structure found in paper **II** as the extent of the study was notably larger and the connectivity via streams was relatively small. The influence of stream connectivity to community similarity gets support from (Liu *et al*. 2013), who concluded that hydrology and the directionality of stream flow have more direct influence on community similarities than overland distances. This finding could further suggest that dispersal via air has a minor significance in structuring stream microbial communities, especially within stream networks.

In paper **II**, the spatial and climate component was the strongest determinant of both diatom and bacterial communities. Soininen (2007) concluded that spatial control may exceed environmental control on microbial communities at spatial scales > 1000 km, which was further sup-

ported by Tang *et al*. (2013). Lear *et al*. (2013) found that bacterial communities exhibited distinct biogeographical patterns at spatial scale < 950 km. The importance of spatial factors for microbial communities may also vary between low and high elevations, as within areas characterized by more evident dispersal barriers such as mountains, the spatial component may be more influential (Bottin *et al*. 2014). Furthermore, at a regional to global scale, historical factors control diatom richness through dispersal (Vyverman *et al*. 2007). Reflecting the theory of island biogeography and the metacommunity concept (MacArthur and Wilson 1967, Leibold *et al*. 2004), the communities in isolated areas should be less diverse and harbor unique communities (Vyverman *et al*. 2007). Thus, samples collected from isolated and extreme environments will likely have a pronounced effect on the importance of environmental and spatial factors structuring the communities, which needs to be acknowledged. The results of this thesis indicate that microbial communities are spatially structured even at much smaller spatial extents than generally suggested (Soininen 2007), also within continental or regional scales.

The importance of spatial processes for insect genus richness differed remarkably between the boreal and tropical regions (**IV**). Spatial variables were notably more important in Brazil than Finland. This result was unexpected especially considering the smaller spatial extent of the study area in Brazil and may be related to higher beta-diversity in the tropics than in boreal regions (Rodriguez and Arita 2004, Qian *et al*. 2005, Qian and Ricklefs 2007). In addition, this finding may be a result of dispersal limitation related to voltinism, as large-bodied univoltine genera may exhibit dispersal limitation (Saito *et al*. 2015). Alternatively, the spatial effect may also be caused by mass effects as noted for diatoms above (Leibold *et al*. 2004, Astorga *et al*. 2012), or spatially structured unmeasured environmental variables. Similarly to genus richness, the effect of spatial factors for insect abundance varied between the regions, being notably important in Brazil, but negligible in Finland (**IV**). The reasons causing this difference remain speculative at present and could be related to some unmeasured spatially-structured environmental variables that were important in the tropics, but not in the boreal region. Regardless, this discrepancy is significant enough to deserve further examination.

4.2.6 Climate

In addition to local abiotic and biotic variables and catchment characteristics, climate also influenced stream microbes. Both microbial groups were associated with climatic variables, diatoms with GDD, GSP and WAB and bacteria with GSP and WAB (**II**). Species richness in both microbial groups was positively associated with GDD. The direction of this relationship may not be straightforward though, as Pajunen *et al*. (2017) found a strong negative relationship between diatom species richness and GDD at spatial scale of > 1000km. The results of paper **III** could further support this view, as tropical diatom species richness did not exceed that of boreal streams. In general, the climatic influence is expected to be highly dependent on the spatial scale, as the range of climatic variables increase with increasing geographical distance, and consequently, community variation is likely to increase as well. Moreover, the relative contributions of environmental and spatial variables to microbial community variation are likely to be scale-dependent (Tang *et al*. 2013) and context-dependent (Heino *et al*. 2012).

The variation in microbial communities is typically notoriously hard to explain, which was also evident by the low explanatory power of the models (**I** – **III**). This result was also probably affected by the very high number of OTUs and

the fact that bacterial communities comprised many functionally different taxa such as producers and decomposers. These groups are likely to be driven by different factors, which further suggests that caution should be taken when bacterial community are considered as a single entity. The low explanatory power of the models did not only apply to microbial communities, as this was also true for stream insects (**IV**). Although this may be related to some unmeasured environmental factors that are yet to be elucidated, a more probable explanation may be related to temporal fluctuations of stream communities that we could not address using snapshot sampling design. Indeed, the small explanatory power is likely to be related to the fact that stream communities are affected by joint effects of various complex interacting factors (Allan 2004, Lear and Lewis 2009, Low-Decarie *et al*. 2014), which fluctuate also through time. In addition, a large amount of unexplained variation may be related to stochastic processes that shape microbial communities.

4.3 Benthic diatom diversity patterns and the underlying factors within and among streams and stream orders (I, III)

4.3.1 Diatom community variation within and among streams

Although widely used in biomonitoring, benthic diatom diversity patterns are not fully understood. This is especially true for tropics, intermediate spatial scales and across stream orders. Furthermore, variation in benthic diatom community composition within streams has received surprisingly little attention but see Hollingsworth and Vis (2010). The large variation in community composition within streams (**I**) encourages biomonitoring programmes using benthic diatoms to include more than one riffle site from a stream into the sampling efforts in order to cover an adequate fraction of the whole community. Diatom communities within a stream seem to be more similar than among streams as shown through significant spatial autocorrelation and CAP-ordination (**I**). Hence, connectivity and unidirectional stream flow between the sampling sites logically promote community similarity for passively dispersed organisms (Liu *et al*. 2013), which is further supported by Zorzal-Almeida *et al*. (2017) who found connectivity to be a significant driver for diatom species composition. However, among-stream differences in diatom communities can be significant even in a relatively small area (**I**). This finding suggests that streams are influenced by variable physical and chemical characteristics depending on a range of variables at the catchment level and further harbour distinct communities, thus exhibiting uniqueness. Furthermore, the contribution of aerial passive dispersal to variation in diatom communities within catchments may be weak.

4.3.2 Diatom species richness and beta diversity patterns. The importance of headwater streams for regional diatom diversity

Diatom species richness increased from headwaters to medium order streams (**III**) and thus, gives support to the RCC and to results reported by Stenger-Kovacs *et al*. (2014). However, the uniqueness of the benthic diatom communities was significantly higher in headwater streams than in medium order streams, which may imply that the deteriorating effect of human activities due to the increase of potential stressors was large enough in streams of medium order to homogenize stream biodiversity. This result is further supported by Passy and Blanchet (2007) who found diatom species richness to be higher in unstable stream reaches, whereas beta diversity was significantly higher in geomorphically stable reaches. Higher diatom species richness can also

be related to higher amount of resource availability (Pajunen *et al*. 2017), which is expected to prevail at higher order stream sites due to higher nutrient concentrations and light intensities. However, as concluded in paper **I**, sampling design in papers **II** and **III** encompassing only one riffle site may have underestimated species richness in streams with high gamma diversity.

The unique diatom communities found from headwater streams (**III**) was an interesting result and deserves more thorough discussion from a conservation point of view. Headwater streams are characterized by hydrological independence and ecological autonomy (Lowe and Likens 2005), and spatial isolation may be the key mechanism promoting higher beta diversity in these systems (Finn *et al*. 2011). Unique headwater communities should encourage headwater stream conservation, which is emphasised by other studies that reported similar findings for macroinvertebrates (Finn *et al*. 2011), fish (Paller 1994) and for the whole biofilm communities (Besemer *et al*. 2013). This view is further supported by Saunders *et al*. (2002) who concluded that at the catchment scale, conservational efforts should focus on headwater streams, since not only will this benefit upstream sites, but also downstream sections of the stream, which are dependent on upstream flow as 90% of the discharge may be from headwaters (Kirkby 1978 cited by Haycock *et al*. 1993). This approach, however, is dependent on the connectivity of the stream network as conservation efforts aimed at headwaters will not benefit downstream sites if the stream network is disconnected by dams or water falls, for example (Saunders *et al*. 2002).

The degree of beta diversity varied significantly between streams even at intermediate spatial scale and community variation was larger than habitat heterogeneity among streams (**I**), which could suggest that beta diversity was driven by some unmeasured variables. Alternatively, differences in beta diversity might be related to temporal variability of some environmental or biotic factors. For example, snapshot sampling could not take into account disturbance regime or biotic factors, such as priority effects, which might have had significant influence on diatom communities. Beta diversity was higher in headwater streams than in mid-order streams and, of beta diversity components, species turnover was dominating, whereas nestedness was notably smaller (**III**). In addition, species turnover was higher in headwater streams, whereas nestedness component increased downstream indicating that communities downstream were less unique. Piano *et al*. (2017) found similarly species turnover to dominate beta diversity components during water scarcity in Mediterranean streams and, thus, it could be argued that species turnover component is likely to dominate in conditions where stream sections are disconnected. However, nestedness in freshwaters is found to be overall relatively weak, while freshwater systems promote high species turnover in general (Heino 2011).

Conductivity, pH and temperature were important variables affecting diatom species richness and LCBD. These variables increased with increasing stream order, and, thus, stream order may summarize some important physical variables of a stream and act as a surrogate for diatom species richness and the uniqueness of the communities (**III**). This proposal is supported by Stenger-Kovacs *et al*. (2014) who found higher diatom species richness from larger streams. In large streams human impact typically increases as well, which can lead to highly nutrient rich and polluted streams and such environments likely harbor only few species adapted to the extreme conditions (Smucker and Vis 2013). The range of the measured environmental variables may have a profound effect on the relationship of species richness and the variable under study. When en-

vironmental gradient is large, species richness is likely to peak at the intermediate levels, showing unimodal relationship (Yang *et al*. 2015). Diatom species richness peaked at the intermediate levels of agriculture (**II**) and temperature (**III**) supporting this view. However, spatial scale can have a significant effect on the relative importance of environmental variables, as the range of the variables under study is reflected at these scales (Martiny *et al*. 2011) and needs to be taken into account in studies aiming to disentangle factors contributing to community variation.

4.4 The effect of environmental heterogeneity on benthic diatom beta diversity (I, III)

Beta diversity was not related to environmental heterogeneity at intermediate spatial scales (within a stream, **I**), whereas at a larger spatial scale, a significant positive relationship was found (**III**). This discrepancy is likely to be caused by the fact that heterogeneity typically increases with increasing geographical distance. This result further stresses the effect of spatial scale on the detection of ecological patterns and the underlying mechanisms (Levin 1992, Palmer and Poff 1997). Differences in environmental conditions between the sampling sites promote variation in community compositions (Gabriel *et al*. 2006, Passy and Blanchet 2007, Astorga *et al*. 2014) and within ecoregion environmental control can be masked by high dispersal rates (Heino *et al*. 2015a). Thus, the most appropriate scale to study diversity-environmental heterogeneity relationships may be across multiple region units (Heino *et al*. 2015a). Data in paper **III** included headwater sampling sites, which harboured unique diatom communities, whereas in paper **I** the sampling sites within a stream were larger and adjacent, and thus well connected. This difference in sampling scheme might have contributed to the contradicting results. Furthermore, differences in water chemistry may have resulted in the positive relationship in paper **III**. However, in paper **I**, water chemistry did not vary substantially between sites within a stream and therefore was not included in analyses. Stream physical and chemical factors were considered as environmental heterogeneity here, whereas temporal heterogeneity could not be addressed.

As the spatial and temporal heterogeneity of the physicochemical environment can considerably interact with the spatial and temporal heterogeneity of the biotic patterns, such as abundance and biomass (Palmer and Poff 1997), the results in papers **I** and **III** might have only revealed a glimpse of the importance of environmental heterogeneity on the stream biodiversity. Overall, however, the positive relationship between habitat heterogeneity and diatom beta diversity emphasises the importance of diverse stream habitats in sustaining biodiversity. Consequently, stream conservation efforts could benefit from retaining environmental heterogeneity. As stated above, this task may be facilitated by focusing on headwater conservation, but the success of this effort may depend on the connectivity of the stream network.

4.5 Comparison of the diversity patterns of stream diatoms and insects in boreal and tropical regions (III, IV)

4.5.1 Diatoms

No evidence was found that tropical streams harboured more diatom species than boreal streams (Appendix B in **III**) even when identical sampling methods were used. Several factors may have contributed to this result. Firstly, following the well-recognized species-area relationship (Preston 1962), the larger sampling area in Finland was likely to result in higher number of observed species. However, the gamma diversity

did not decrease notably by selecting only the 67 southernmost sampling sites in Finland, considering thus identical number of samples. Secondly, tropical area in Kenya harboured only a few freshwater systems. Habitat availability and connectivity between habitats are found to promote species richness as local extinctions are balanced by high rates of colonization (Vyverman *et al*. 2007). Taita Hills is located in the middle of savanna plains, which stay dry most of the year. Thus, the surrounding area contains only few freshwater habitats where colonists could arrive, which could further have an impact on local species richness. Thirdly, latitudinal diversity gradient for diatoms may not be linear from high latitudes to the equator as Vyverman *et al*. (2007) found the relationship of diatom richness and latitude to show different patterns regionally, and further, that there was an interhemispheric asymmetry in local and regional species richness. Thus, factors contributing to micro-organism diversity patterns may act at regional scales and further hamper the efforts to find latitudinal diversity gradient at global scale (Soininen *et al*. 2016).

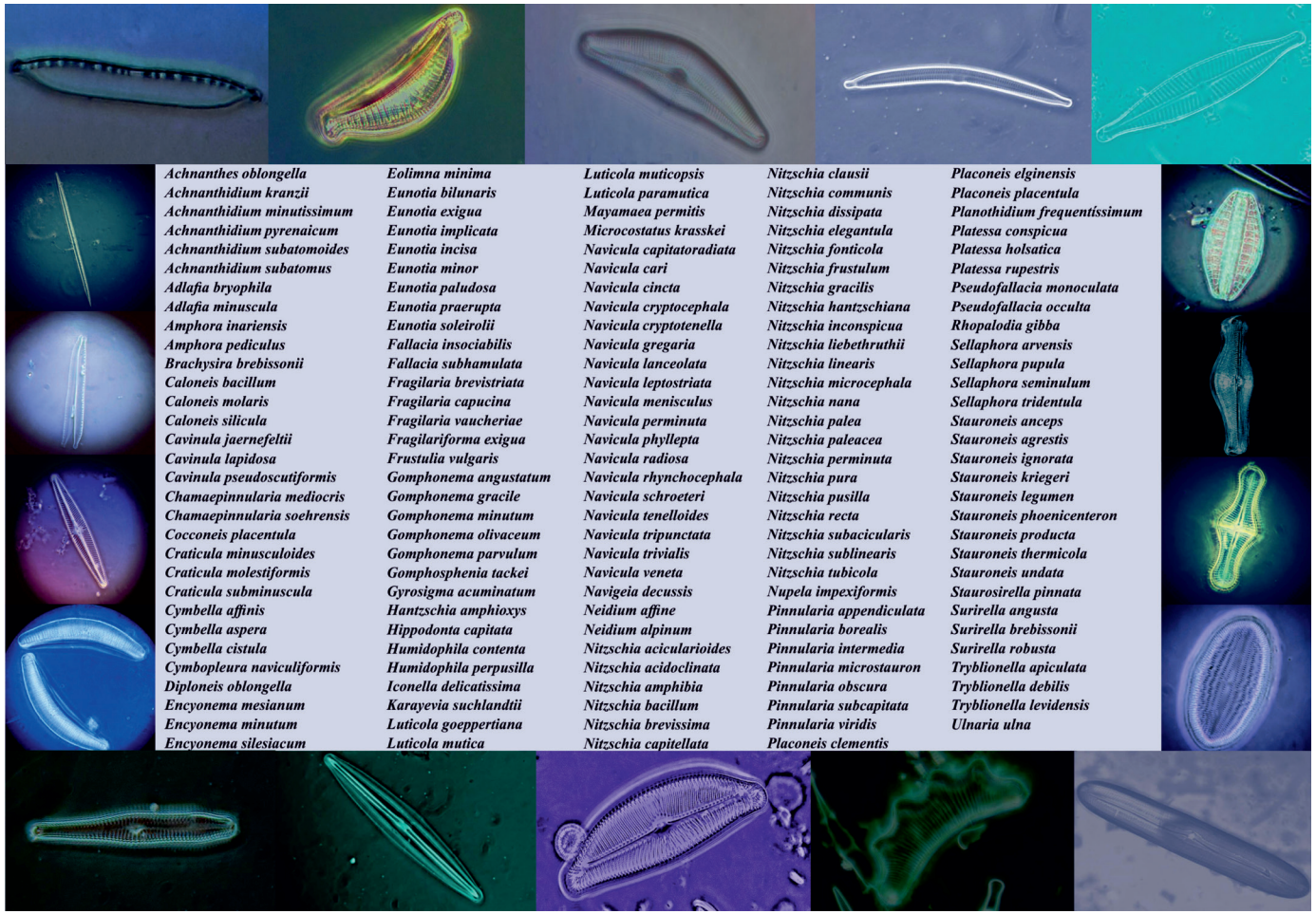
Boreal (**II**) and tropical (**III**) datasets shared 154 diatom species (Table 4), which is more than half of the total number of species (297) observed in tropical samples. By contrast, not a single insect species was shared between Brazil and Finland. This result may emphasise the different dispersal potential of these organisms. Also, diatoms may include more generalist species than stream insects. Why only some micro-organisms show global distributions, could be related for example to the vast population densities, larger niches (environmental preferences) and small size of the cosmopolitan species compared to the rare species. However, the possible errors in morphological species identification can add uncertainty to the results, which is further increased by the presence of cryptic species and phenotypic plasticity (Vanormelingen *et al*. 2008). For example, species identified as *Gomphonema parvulum* may exhibit morphological varieties that should be assigned to other species of the genus, and further that the ecological tolerances of *G. parvulum* should be re-evaluated as there can be notable variation in the ecological responses within the morphological spectra (Rose and Cox 2014). Our results supported this view as *G. parvulum*, which is typically considered as an indicator of organic pollution, (Kelly and Whitton 1995) was found from nearly every sample in paper **II** (102/105) and **III** (64/67) including non-eutrophic sites. By using both molecular and morphological methods, Abarca *et al*. (2014) observed four biogeographically separated taxa of *G. parvulum*, which corresponded to the description of the species and that there was a significant correlation between molecular and geographical distances. Differences in species identification by several individuals may further add uncertainty to the results. However, this source of error was avoided in the present thesis as all diatom species identification was done by the author. The development of molecular methods in diatom species identification will most likely decrease the uncertainties related to species identification and will shed more light into the biogeographical patterns of diatoms.

4.5.2 Stream insects

Only four common insect genera were identified from both regions. The three most common genera in Finland belonged to the orders of beetles, mayflies and stoneflies, whereas in Brazil they were beetles, caddisflies and mayflies. These insect orders are often found to be dominant in stream insect communities (Lancaster and Downes 2013) and, thus these results support the view that their dominance in streams could be a global phenomenon.

The difference in regional insect genus richness between the regions was surprisingly low

Table 4. List of diatom species identified both from boreal (**II**) and tropical (**III**) regions



Achnanthes oblongella	*Eolimna minima*	*Luticola muticopsis*	*Nitzschia clausii*	*Placoneis elginensis*
Achnanthidium kranzii	*Eunotia bilunaris*	*Luticola paramutica*	*Nitzschia communis*	*Placoneis placentula*
Achnanthidium minutissimum	*Eunotia exigua*	*Mayamaea permitis*	*Nitzschia dissipata*	*Planothidium frequentissimum*
Achnanthidium pyrenaicum	*Eunotia implicata*	*Microcostatus krasskei*	*Nitzschia elegantula*	*Platessa conspicua*
Achnanthidium subatomoides	*Eunotia incisa*	*Navicula capitatoradiata*	*Nitzschia fonticola*	*Platessa holsatica*
Achnanthidium subatomus	*Eunotia minor*	*Navicula cari*	*Nitzschia frustulum*	*Platessa rupestris*
Adlafia bryophila	*Eunotia paludosa*	*Navicula cincta*	*Nitzschia gracilis*	*Pseudofallacia monoculata*
Adlafia minuscula	*Eunotia praerupta*	*Navicula cryptocephala*	*Nitzschia hantzschiana*	*Pseudofallacia occulta*
Amphora inariensis	*Eunotia soleirolii*	*Navicula cryptotenella*	*Nitzschia inconspicua*	*Rhopalodia gibba*
Amphora pediculus	*Fallacia insociabilis*	*Navicula gregaria*	*Nitzschia liebethruthii*	*Sellaphora arvensis*
Brachysira brebissonii	*Fallacia subhamulata*	*Navicula lanceolata*	*Nitzschia linearis*	*Sellaphora pupula*
Caloneis bacillum	*Fragilaria brevistriata*	*Navicula leptostriata*	*Nitzschia microcephala*	*Sellaphora seminulum*
Caloneis molaris	*Fragilaria capucina*	*Navicula menisculus*	*Nitzschia nana*	*Sellaphora tridentula*
Caloneis silicula	*Fragilaria vaucheriae*	*Navicula perminuta*	*Nitzschia palea*	*Stauroneis anceps*
Cavinula jaernefeltii	*Fragilariforma exigua*	*Navicula phyllepta*	*Nitzschia paleacea*	*Stauroneis agrestis*
Cavinula lapidosa	*Frustulia vulgaris*	*Navicula radiosa*	*Nitzschia perminuta*	*Stauroneis ignorata*
Cavinula pseudoscutiformis	*Gomphonema angustatum*	*Navicula rhynchocephala*	*Nitzschia pura*	*Stauroneis kriegeri*
Chamaepinnularia mediocris	*Gomphonema gracile*	*Navicula schroeteri*	*Nitzschia pusilla*	*Stauroneis legumen*
Chamaepinnularia soehrensis	*Gomphonema minutum*	*Navicula tenelloides*	*Nitzschia recta*	*Stauroneis phoenicenteron*
Cocconeis placentula	*Gomphonema olivaceum*	*Navicula tripunctata*	*Nitzschia subacicularis*	*Stauroneis producta*
Craticula minusculoides	*Gomphonema parvulum*	*Navicula trivialis*	*Nitzschia sublinearis*	*Stauroneis thermicola*
Craticula molestiformis	*Gomphosphenia tackei*	*Navicula veneta*	*Nitzschia tubicola*	*Stauroneis undata*
Craticula subminuscula	*Gyrosigma acuminatum*	*Navigeia decussis*	*Nupela impexiformis*	*Staurosirella pinnata*
Cymbella affinis	*Hantzschia amphioxys*	*Neidium affine*	*Pinnularia appendiculata*	*Surirella angusta*
Cymbella aspera	*Hippodonta capitata*	*Neidium alpinum*	*Pinnularia borealis*	*Surirella brebissonii*
Cymbella cistula	*Humidophila contenta*	*Nitzschia acicularioides*	*Pinnularia intermedia*	*Surirella robusta*
Cymbopleura naviculiformis	*Humidophila perpusilla*	*Nitzschia acidoclinata*	*Pinnularia microstauron*	*Tryblionella apiculata*
Diploneis oblongella	*Iconella delicatissima*	*Nitzschia amphibia*	*Pinnularia obscura*	*Tryblionella debilis*
Encyonema mesianum	*Karayevia suchlandtii*	*Nitzschia bacillum*	*Pinnularia subcapitata*	*Tryblionella levidensis*
Encyonema minutum	*Luticola goeppertiana*	*Nitzschia brevissima*	*Pinnularia viridis*	*Ulnaria ulna*
Encyonema silesiacum	*Luticola mutica*	*Nitzschia capitellata*	*Placoneis clementis*	

considering the expectation of tropics harbouring more diverse communities (Rosenzweig 1995, Willig *et al*. 2003). This finding further adds discussion into the debate of whether any latitudinal diversity gradient exists for stream insects (Stout and Vandermeer 1975, Flowers 1991, Jacobsen *et al*. 2008). The reason for this confusion may be related to the fact that some insect orders may follow the latitudinal diversity gradient, whereas others do not. For example, dragonflies and beetles are demonstrated to be more diverse in the tropics, while the diversity peaks of mayflies, stoneflies and caddisflies are more complex (Brown 1981, Boyero *et al*. 2009). The richness of mayflies peaks at 30°S, 10°N and 40°N and the richness of caddisflies seems to be highest near the equator and at 40°N and 40°S (Vinson and Hawkins 2003). In addition, the distributions of some stoneflies seem to be mainly confined to temperate areas (Jacobsen *et al*. 2008). In the present study, dragonflies, beetles and also mayflies were more regionally diverse in Brazil, whereas the regional genus richness of stoneflies and caddisflies was higher in Finland. Hence, it seems that examining latitudinal diversity patterns for a large group of organisms containing different taxa with varying ecological preferences may not be a meaningful approach and aims to find these patterns should instead focus on specific taxa. In order to compare richness of different streams reliably, standard sampling areas should be used. Therefore, it needs to be acknowledged that the size difference in sampling areas between Finland and Brazil may have caused some uncertainty in the results (Vinson and Hawkins 2003) and is under our current study.

Common and rare genera exhibited similar patterns for both regions as the rank-abundance curves were similar (Fig. 3 in **IV**) both including five common and several uncommon genera, which is a frequent phenomenon in nature and is also observed at the species-level (Siqueira *et al*. 2012). Thus, to find similar patterns from both regions was not surprising. Why few taxa are exceptionally abundant, whereas most remain rare is explained by differences in the environmental preferences (Magurran and Henderson 2003) and functional traits (Cornwell and Ackerly 2010). However, Siqueira *et al*. (2012) reported common and rare genera both to respond to environmental factors, but concluded that the direction of the responses may be opposite, which is supported by Lennon *et al*. (2011).

The large difference in regional insect abundances between the regions was a surprising result. The results indicated that a high insect abundance may not guarantee high genus richness in boreal areas, whereas in the tropics genus richness can be high even based on lower abundances. This result contradicts the general view of a strong correlation between richness and abundance (Gotelli and Colwell 2001, Evans *et al*. 2005). However, several factors may have contributed to this result. Stream water TN and TP levels were notably higher in Finland than in the tropics (a result found also in paper **III**), which might be related to the low nutrient levels in old tropical soils (Reich and Oleksyn 2004) and, further, to higher algal productivity and subsequent sources of nutrition in boreal region. Nutrients could also contribute to the abundance differences via allochthonous inputs as leaf litter in tropics may have lower nitrogen and phosphorus concentrations and thus be less nutritious food source for shredding invertebrates (Boyero *et al*. 2011). In addition, the decomposition dynamics of leaves may differ between tropics and temperate areas through phytochemistry (Aerts 1997) and that tropical leaves contain defensive compounds that increase with leaf age providing protection especially against insects (Coley 1988). Furthermore, in contradiction with the assumption of higher temperature regime promoting

higher productivity and species richness, insect abundances may actually decrease with increasing temperatures as shown through increasing altitude (Yule *et al*. 2009) and latitude (Boyero *et al*. 2011).

The patterns of local richness and abundance were similar to regional richness and abundance. Local genus richness was somewhat higher in Brazil than Finland and abundance was notably greater in Finland than in Brazil; both, however, showing a large variation within each region. These results indicate that regional and local factors act in concert in determining local insect richness and abundance, further stressing the importance to take into account factors that operate at different scales. Such regional factors are glacial history and temperature-related evolutionary rates to name a few, which should affect boreal communities more strongly than tropical ones. The upper limit to local genus richness is determined by regional factors, and local richness is further controlled by environmental variables that can show large spatiotemporal variation within and between regions resulting in subsequent variation in richness and abundance. The efforts to find higher species richness from tropics may also be confounded if local species richness does not correlate with regional species richness, which may be related to the interactions between evolutionary/biogeographic processes and local ecological/stochastic processes (Craig 2003).

It should be noted that identifying insects to the species level might have led to a different result, but it was virtually impossible due to the taxonomic impediments mentioned earlier. However, as richness relationships from species to family level are shown to be conserved for most organisms (Hubbell 2001), this might have not been the case. The observed patterns for insect local and regional richness and abundance may vary seasonally. This seasonal variation is certainly the case in Finland where stream insect life cycles follow distinct seasons, but perhaps also for Brazil between wet and dry seasons. Therefore, sampling in spring in Finland and both dry and wet seasons in Brazil might have resulted in greater genus richness and different patterns in insect abundance. There is evidence that insect abundance may be greater in the tropics during dry season (Pearson *et al*. 2017) but also contradictory studies that found no seasonal difference in the tropics (Melo and Froehlich 2001, Siqueira *et al*. 2008, Tonkin *et al*. 2016). However, due to the significant difference in insect abundances between Brazil and Finland, this difference is likely to be real irrespective of the sampling season and most certainly requires the attention of further studies. Insect richness and abundance varied strongly among streams within the same region suggesting that streams cannot be categorized into 'boreal' or 'tropical' based on insect communities (Dudgeon 2008). Thus, the within-region differences may affect the abundance and richness more than the biome and further emphasises the unique nature of each stream.

5 Conclusions and future perspectives

This thesis increased the understanding of the spatial variation of stream communities in boreal and tropical regions and shed further light on the underlying factors. The thesis demonstrated that stream communities are controlled by a wide range of factors at multiple spatial scales. Local environment, catchment characteristics and spatial and climatic factors contributed solely and jointly to stream community variation and richness. Water chemistry and stream physical variables had significant influences on microbial communities and species richness as well as on insect genus richness and abundance. Partly the

same environmental variables were important for diatoms and insect genus richness in both boreal and tropical regions, whereas the most important variables driving local insect abundance varied between the regions. In addition to abiotic factors, also biotic factors were important in structuring diatom communities, as the number of grazers had a significant effect on diatom communities and morphological groups across multiple sites within a stream. Local abiotic and biotic variables can exhibit notable temporal fluctuations, which can further have a significant impact on stream communities. Since the temporal fluctuations could not be addressed in this thesis, this aspect could be an important and interesting topic to study in boreal and tropical regions in the future.

Catchment characteristics, especially agriculture, significantly influenced microbial communities and species richness, which emphasizes the effects of anthropogenic activities on stream microbial communities. Catchment characteristics act at larger spatial scale than local environmental variables and influence stream microbial communities indirectly via water chemistry. Furthermore, they can reflect water chemistry at longer time scales and, thus, be more robust determinants of biotic communities. One of the future aims would be to study the effect of land use on stream insect communities in boreal and tropical regions.

Stream microbial communities exhibited significant spatial variation at spatial scales smaller than continental or global, emphasizing that microbial communities are not solely controlled by local environmental variables. Spatial processes also had a significant effect on insect genus richness in the tropics, but not in the boreal study region. The precise mechanisms causing these between-region differences is yet unresolved and will be in the scope of future studies. Diatom community composition exhibited large variation within streams at intermediate spatial scale, which could be an important issue to take into account in biomonitoring programs. The among-stream differences in diatom community composition suggest that connectivity and unidirectional stream flow promote community similarity within streams and, further, that aerial dispersal within catchments may be weak.

Diatom species richness and community uniqueness were related to stream order, which could possibly be used as a surrogate for these biotic variables, or at least serve as a basis for biotic stream classification. Diatom beta diversity and community uniqueness peaked in headwater streams, which should encourage headwater stream conservation. Stream size was also positively related with insect genus richness in both tropical and boreal regions, suggesting its global importance for insects. The importance of environmental heterogeneity on diatom beta diversity varied depending on the spatial scale and measured environmental variables. Overall, the positive effect of environmental heterogeneity on diatom beta diversity emphasizes the importance of habitat heterogeneity in sustaining biodiversity.

Diatom species richness was not higher in the tropics than in the boreal study region, suggesting that diatoms may not follow traditional global latitudinal diversity gradient. More than half of the diatoms found from the tropics were also found from the boreal study region, whereas not a single insect species was shared between tropical and boreal regions. This finding may emphasize the different dispersal potential of these organisms and suggest that some micro-organisms exhibit cosmopolitan distributions. Taxonomic impediments and phenotypic plasticity may add uncertainty to the results, but species identification using molecular methods in the future may alleviate these uncertainties. One aim in the future studies is to examine diatom biogeography using

samples from a number of oceanic islands, and combine morphological and molecular methods. Local and regional insect genus richness were slightly higher in Brazil than in Finland, whereas local and regional insect abundance were notably greater in Finland than in Brazil. Factors related to evolutionary diversification may explain differences in genus richness, whereas nutrient concentrations may cause the observed difference in abundance between the regions. The within-region variation in genus richness and abundance was notable among streams, which emphasizes that stream categorization based solely on the region may be artificial.

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